

THE MOUNTAIN VIPERS OF THE MIDDLE
EAST — THE *VIPERA XANTHINA* COMPLEX
(REPTILIA, VIPERIDAE)

by

G. NILSON and C. ANDRÉN



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ABSTRACT

Univariate and multivariate analyses of 26 morphological characters — recorded from 228 preserved or living vipers, or in some cases exuvia, representing 25 populations — suggest the formation of two phenetic groups, based mainly on the scalation of the head. The *xanthina* species-group, containing *Vipera xanthina* in western Turkish Anatolia and easternmost Greece, *V. bulgardaghica* in Cilician Taurus and south Central Anatolia, *V. bornmuelleri* in Lebanon and adjacent Syria, and *V. wagneri* in north-eastern Iran, is characterized by having supraoculars in broad contact with the eye and a single canthal scale on each side of the head. The *raddei* species-group, containing *V. latifii* and *V. albicornuta* in northern Iran, and *V. raddei* in northwestern Iran, eastern Turkey and parts of the adjacent USSR, is characterized by having supraoculars raised and angled, and separated from the eye by a complete circumocular ring, and by having two or more canthals on each side of the head. A new subspecies *Vipera raddei kurdistanica* **ssp.n.** from northwestern Iran belongs to this species-group.

A character analysis is performed, and inter- and intraspecific morphological variation is analysed and discussed, with concentration on *xanthina*, *bornmuelleri*, and *raddei* which are shown to be the most variable taxa.

A detailed description of the external morphology and diagnosis of each taxon is given. Holotypes, syntypes, or topotypes of all taxa have been included in the study. Data on reproduction and habitat are presented, the total distribution of the taxa within the complex is clarified, and a key to the species, subspecies, and subgroups is given.

The phylogenetic cladistic analysis indicates that *V. bulgardaghica* is the sister species to all other taxa in the complex. Further, *V. bornmuelleri* is a sister species to *wagneri*, *xanthina*, and the *raddei* species-group. *Vipera xanthina* alone is the sister group to the *raddei* species-group. The latter group is monophyletic while the phenetic *xanthina* species-group is paraphyletic.

Theories of zoogeography and evolutionary pattern are discussed. The present zoogeographic pattern is mainly explained by vicariance models, but the occurrence of *V. xanthina* in western Anatolia and Greece is explained by dispersion in geologically recent times.

INTRODUCTION

The Mountain Vipers of the Near and Middle East, the *Vipera xanthina* complex, is a group of vipers which is morphologically and geographically intermediate between the smaller European species within the genus and the larger ones of the *lebetina* s. l. group. This assembly of rather rarely seen taxa is distributed in extreme southeastern Europe, Asia Minor, the adjacent USSR, and parts of western Asia. Many of the taxa have a very restricted occurrence within this area. Together with the *russelli* complex

(*russelli* and *palaestinae*), the *lebetina* complex, *Pseudocerastes* and *Eristicophis*, they contain several derived character states which separate them from the *berus* (*ursinii*, *berus*, *seoanei*, *kaznakovi*, *barani*) and *aspis* (*latasti*, *ammodytes*) groups, as shown by Groombridge (1980). Some of these characters are partial re-fusion of the nasal and prenasal, dorsal head scalation, presence of an azygos anterior vein, and a reduction of the occipital branch of the *Musculus depressor mandibulae* (Groombridge 1980).

Traditionally in the literature, *raddei* has been treated as a subspecies of *Vipera xanthina*. This can be traced back to papers by Mertens (1951, 1952), where he also included *palaestinae* in this "Rassenkreis". The Iranian *Vipera latifii* described in 1967 (Mertens et al.) was incorporated in the group on species level as closely related to *Vipera xanthina raddei*. The same year Mertens (1967) also raised *Vipera bornmuelleri* from synonymy of *xanthina* to species rank, indicating that it was sympatric with *xanthina* (through *x. palaestinae*).

The geographically close *Vipera palaestinae*, which is a lowland species, is however more related to *Vipera russelli* than to the taxa in the *xanthina* complex, due to several characters such as prefrontal form and increased size. The *palaestinae* and *russelli* are a monophyletic group united further by a similar pattern on head and body, nasal scalation, snout shape, and a reduction (*palaestinae*) and absence (*russelli*) of peritoneal pigment (darkly pigmented in most vipers and in other Eurasian species) (Groombridge 1980). This is probably a derived state and shows a strong phenetic resemblance.

Thus Groombridge (1980) suggested the more satisfactory solution to the systematics of this group by showing that *palaestinae* is not only a good species but also more related to *russelli* and hence belongs to the *lebetina* branch. Further, he suggested that *bornmuelleri* should be treated as a subspecies of *xanthina* and with *raddei* and *latifii* as good species.

In a parallel study on venom comparisons and crossbreeding (Nilson & Sundberg 1981) a similar result was obtained with separation of *xanthina*, *raddei*, and *palaestinae* as well as *latifii* on species level. *Vipera bornmuelleri* was not included in this study, in the absence of living specimens at that time. In a previous study Weinstein and Minton (1984) compared lethal potencies and immunoelectrophoretic profiles of venoms of *bornmuelleri* and *latifii*, and the results led them to envisage a considerable separation in evolutionary development between these two taxa.

The present work is a further development of the last views, now taking all available populations into consideration.

In a paper by Obst (1983) a different model of the systematics of this group was suggested, with the *xanthina* as one species and *raddei* as the second, where *latifii* and *bornmuelleri* are included as subspecies of *raddei*. This is, however, not a suitable solution in view of the morphological patterns obtained so far. Obst (op.cit.) also suggested the reintroduction of the generic name *Daboia* for the *xanthina* complex and the other advanced vipers of the Middle East, including *Pseudocerastes*.

It has, however, convincingly been demonstrated by Groombridge (1980) that a diphyletic hypothesis of the genus *Vipera* must be rejected in favour of a more 'pectinate' phylogeny for the smaller european vipers, with the main stem leading toward the *xanthina* group and onwards. This contradicts a generic division of *Vipera*.

The term "species-complex" is here used for the entire group of species related to *xanthina* as defined below, and is equivalent to the *russelli* and *lebetina* complexes of advanced Oriental vipers of the genus *Vipera*. The term "species-group" is used for the smaller assemblage of closely related species and subspecies of vipers of phylogenetically recent origin, and where incipient speciation is taking place or has just been finished.

Two species within the *xanthina* complex, as currently recognized, and named prior to the twentieth century are

V. xanthina (Gray, 1849)

V. raddei Boettger, 1890.

A third species also named during the last century but until recently hidden under synonymy (Mertens 1967) is

V. bornmuelleri Werner, 1898.

The fourth species was described 1967 from Iran under the name

V. latifii Mertens, Darevsky & Klemmer, 1967.

Three additional species within the same complex were discovered during 1983, when we encountered specimens from different museums and collections for this study (Nilson & Andrén 1984 b, 1985 a, 1985 b):

V. albicornuta Nilson & Andrén, 1985

V. wagneri Nilson & Andrén, 1984

V. bulgardaghica Nilson & Andrén, 1985.

The finding of previously unknown taxa can be predicted in genera and from regions where collecting by different reasons is problematic, and in groups where very few specimens are available. The mountain vipers of the genus *Vipera* belong to such taxa, in many cases rarely seen, and have so far not been subjected to any separate revision based on adequate material. The purpose of this study, as part of a continuing analysis of relationships within the genus *Vipera* and related groups of vipers, is to rectify this situation.

The main purposes of the work are to

1. analyse patterns of geographic variation in external morphological characters,
2. define the members of this complex taxonomically,
3. develop a phylogeny of taxa in the complex, and to
4. make a hypothetical reconstruction of the biogeographical evolution.

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Recently collected series from the whole area made it possible to do a detailed taxonomic study of this group of species. In fact, the present investigation could not have been done without the extensive collections made by Dr. M. Latifi in Iran and Mr. H. B. Cott in Lebanon, which are deposited in Razi State Institute at Teheran and in the British Museum respectively, as well as the rich material in the Leningrad Zoological Institute.

Besides, some small series were available from Syria, Turkey, Greece, and the USSR, in different museums and private collections.

Parts of the material, as well as ecological information, were collected by the authors during several field trips to Turkey and Iran. Collected vipers were normally brought back alive to Göteborg and, in many cases, were successfully bred at the Department of Zoology. One or both of the authors visited western Turkish Anatolia during 1968 and 1970, and different parts of the Turkish province Antalya in 1972, 1973, 1981 and 1982. Help was obtained by Nils Hallenberg during a stay in Ciglikara, province Antalya, in 1973. We performed additional field studies together with Börje Flärdh in the eastern Taurus range and central Anatolia during 1983 and 1984. The Alburz mountains and Zanzan valley in Iran were visited in 1973, together with Margareta Nilson and Björg and Bengt Silverin, and in 1976 together with Björn Gullander, Christer Hall and Anders Börjeson. All accompanying persons are gratefully acknowledged for valuable help in the field.

Leif Westrin is thanked for technical assistance, Liselotte Öhmann and Aino Falk-Wahlström for art and drawings. All studio and laboratory photographs were taken by Håkan Berg (GNM) to whom we are very grateful. Björn Rosander and Irene Isaksson kindly supported us with statistical help.

Thus, much preserved material and living specimens of *Vipera*, from the collection at the Department of Zoology, University of Göteborg (ZIG), have been used for comparison in this study. Additional material originates from Dr. Wolfgang Böhme (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn), Dr. Mahmoud Latifi (Razi State Institute in Hesarak/Teheran), Mrs. Christine Stocker (Naturhistorisches Museum, Basel), Drs. Ilya Darevsky and Nikolai L. Orlov (Zoological Institute, Academy of Sciences, Leningrad), Drs. Frans Tiedemann, Josef Eiselt and Michael Häupl (Naturhistorisches Museum Wien), Dr. W. Ronald Heyer (National Museum of Natural History, Smithsonian Institution), Dr. Volker Mahnert (Muséum d'Histoire Naturelle, Genève), Dr. E. N. Arnold (British Museum, Natural History, London), Dr. Sherman A. Minton (Indiana University), Prof. Heinrich Mendelssohn (Tel Aviv University), Mr. Börje Flärdh (Stockholm), and from the Natural History Museum in Göteborg. All these persons and institutions are gladly acknowledged. Zoogeographical information was also generously given by Mr. Hans Triet (Bern) and Mr. Herbert Billing (Zürich).

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Abbreviations for museums and private collections as used in the text are:

BFC	Börje Flärdh collection, Stockholm
BM	British Museum (Natural History), London
GNM	Göteborg Natural History Museum, Göteborg
HUJR	Hebrew University of Jerusalem
MHNG	Muséum d' Histoire Naturelle, Genève
NMB	Naturhistorisches Museum, Basel
NMW	Naturhistorisches Museum, Wien
RSI	Razi State Institute, Hesarak/Teheran
SMF	Naturmuseum und Forschungs-Institut Senckenberg, Frankfurt am Main
SMC	Sherman A. Minton Collection, Indianapolis
TAU	Tel Aviv University
USNM	Smithsonian Institution, Washington, D. C.
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn
ZIG	Department of Zoology, University of Göteborg, Göteborg (authors' collection, which later will be incorporated in GNM)
ZIN	Zoological Institute, Academy of Sciences, Leningrad
ZSM	Zoologische Staatssammlung München.

MATERIAL AND MEASUREMENTS

Altogether 228 snakes within the complex have been examined. For most of these, 32 different data have been collected, and 26 of these have been used in the multivariate analyses. In a few cases, only exuvia from mainly captive animals in different possessions were available to us, and in some museum material only half snakes or heads have been preserved. In these cases a reduced number of characters was measured. The following characters were used directly or when calculating relative values:

- Total length
- Tail length
- Number of ventrals, following the Dowling (1951) method
- Preentrals, defined as those gular scales anterior to ventrals which were broader than long
- Number of subcaudals

- Number of anterior dorsal scale rows, counted one head length posterior of head
- Number of midbody dorsal scale rows, counted at the exact middle of the body
- Number of posterior dorsal scale rows, counted one head length anterior to anal
- Number of apical plates in contact with the rostral
- Interocular row of scales, counted between anterior parts of supraoculars
- Number of intercanthal scales, which are all scales between the canthals, supranasals, and apicals
- Number of intersupraocular scales, which are all scales between the supraocular plates
- Number of canthals, counted as sum of right and left sides
- Supraoculars are angled or not
- Occurrence of supraciliar scales, i.e. whether or not inner circumocular rings are separating the eyes from the supraocular plates
- Number of scales in first circumocular ring, i.e. all scales in contact with the eye except the supraocular plate in those cases when supraciliar scales are missing. Counted as right and left side together if nothing else is stated
- Number of scales in second circumocular ring, which are all scales in contact with and lying distal to the scales in the first circumocular ring. They are counted from the one that is in contact with the canthal anterior to the eye, or with the elongated upper anterior preocular, below and around the eye and ending with the scale that is in contact with the posterior end of the supraocular plate; counted as right and left side together if nothing else is stated. In those comparatively few cases when one of the two circumocular rings on each side is broken below the eye, and resulting in a single subocular row, the scale in this single row is incorporated in that circumocular ring of which it is a natural and major part
- Number of subocular scales, at shortest distance between eye and supralabials
- Upper preocular plate in contact with the nasal or separated from it by a loreal (which is then the first scale in the second circumocular ring)
- Number of supralabials (right + left)
- Number of sublabials (right + left)
- Number of scales in the transverse mental row posterior to the chin shields and on each side in contact with sublabials
- Number of windings, rhombs or blotches in the dorsal body pattern
- Dorsal pattern reduced or inverted or not, i.e. with the dorsal pattern lighter than the ground colour
- Shape of the neck pattern, which normally consists of two angled spots, which may be reduced or in contact with the dorsal pattern
- Belly pattern, which may be spotted or not.

Localities and number of specimens used in the analyses (Fig. 1):

1. **Istanbul:** The specimens used from this region are from two sources. Two specimens are from Yalova, SE Istanbul (Geyikdere Köyü Kocaboğaz mevki) in Anatolian Turkey (ref. Eiselt & Baran 1970) while one specimen is from the European part of Istanbul (ref. Mertens 1952).
2. **Canakkale:** 5 km south of Kıtılbahtır, European Turkey (NMW 19543). One specimen.
3. **Balıkesir:** Dereköy (ref. Eiselt & Baran 1970). One specimen.
4. **Ankara:** (NMW 15135) Polath, Devlet Üretme Çiftliği (ref. Eiselt & Baran 1970). Two specimens.
5. **Izmir:** Specimens originating from the surroundings of Izmir and Bornova (MHNG 1334.93, GNM 592, NMW 15138, BM 85.9.1.1., and Eiselt & Baran 1970). Five specimens.
6. **Selcuk-Ephesus:** Specimens originating from the surroundings of Selcuk (NMB 20657, ZIG) and from the ancient ruins of Ephesus (Efesus) (NMW 25227 a—c, MHNG 1598.82, ZIG). Eleven specimens.
7. **Aegean Sea:** Specimens from Greek islands close to the Turkish coast in the southern Sporades: Patmos (NMB 18901—2, 20510) and Lipsos (NMB 21037). Four specimens.
8. **Sultan Dagları:** Specimens collected mainly in the surroundings of Akşehir (NMW 19544, MHNG 1354.97—98, 1245.92, ZSM 3216) and in "Sultan Dagi, 200 km SW Ankara" (MHNG 1354.96). Six specimens.

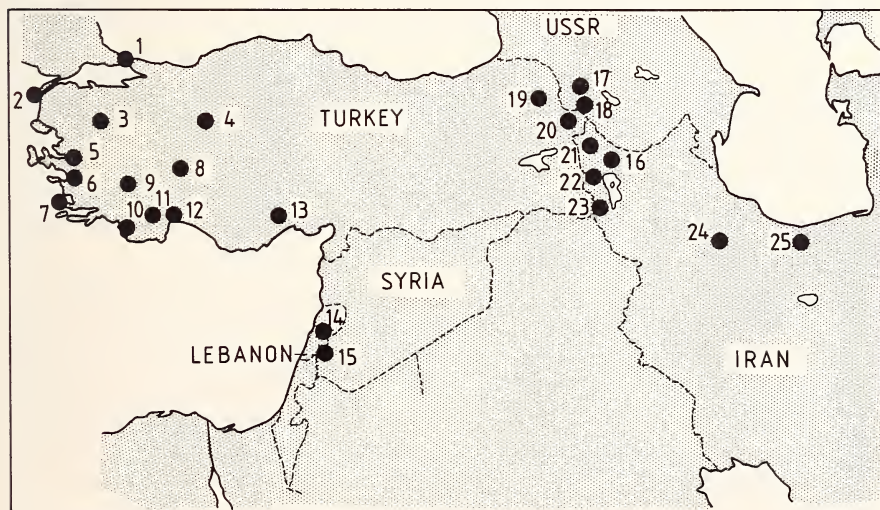


Fig. 1: Sampling localities.

9. **Denizli:** Tavas (ref. Eiselt & Baran 1970). One specimen.
10. **Xanthos:** (= Kinik) about 40 km SE of Fethiye (ZIG, BM 1946.1.18.11.) Six specimens.
11. **Ciglikara:** Specimens originating from the Cedar forest situated about 50 km SSW of Elmali, province Antalya, at an altitude of slightly less than 2000 m (ZIG). Twenty specimens.
12. **Antalya:** Specimens originating from the surroundings of the new harbour of Antalya (ZIG), Gölbaktiche (NMW 13207, vide Basoglu & Baran 1980), Antalya (NHNG 1404.68) and the ancient ruins of Perge (ZIG). Five specimens.
13. **Bulgar Dag:** The Cilician part of the Taurus mountain range, province Nigde. South of Ulukisla. Specimens collected at 2500 m altitude at Kar Boghaz (GNM 1618, NMW 15136, BM 1946.1.19.71). Three specimens.
14. **Bcharré:** Specimens originating from the central parts of Mt. Liban, Lebanon: Bcharré (ZSM 3203), Cedars of Lebanon at 1600 m altitude (BM 1975.1.13.71—81, 1975.1.13.84, MHNG 1333.20—21) and "Zedernwald, ca 2000 m hoch, nördl. Libanon bei Bcharré" (Les Cedrés) (NMW 18826). Nineteen specimens.
15. **Mt. Hermon:** Specimens originating from higher elevations of Mount Hermon on the Lebanese-Syrian border (NMB 21014, 21020, ZIG). Twelve specimens.
16. **Urmia:** Without exactly known origin. Catalogue information says "Von der Armenisch-Persischen Grenze" and Urmia, which is the large lake in province Azarbaidjan, NW Iran, south of the border between USSR and Iran. (ZFMK 23495). One specimen.
17. **Ara-Iler:** USSR, Armjanskaja SSR, Berg Ara-Iler, north of Jerewan (ZIN 19051, 19052, 19054, 19056, 19061, 19185, 19563, 19564, 19567, 19577). Forty-one specimens.
18. **Jerewan:** Specimens collected in the surroundings of Jerewan, Armjanskaja SSR, USSR (ZFMK 17844—17846), Gegard (ZFMK 38130) and Oktemberian (ZFMK 38130). Five specimens.
19. **Digor:** Turkey, province Kars (ZIG). Eighteen specimens.
20. **Ararat:** (Büyük Ağrı Dağı): Collected at higher altitudes (2200 m) on Mount Ararat, Turkey (ref. Flärdh 1983) (BFC, ZIG). Eight specimens.
21. **N. W. Azarbaidjan:** Two specimens from northwest Azarbaidjan, Iran (BM 1976.556—557).
22. **Khoy:** Specimens collected in the Khoy region of province Azarbaidjan, NW Iran (Khoy, Gotor, Razi) (RSI 2841, 2842, 2778, 2789, 2834, 2859). Six specimens.
23. **Rezaeyeh:** Specimens originating from the Rezaeyeh region in west Azarbaidjan, Iran (RSI 3117, 3118, 3128). Three specimens.
24. **Zanjan valley:** Three specimens from the Zanjan region, between Teheran and Tabriz, Iran (Khan chai, Abhar, Zanjan) (RSI 3088, 3098, 3103).

25. **Lar valley:** High alpine valley close to Mount Demavand in central Alburz mountains, south of the Caspian Sea, north of Teheran, Iran: Lar (RSI 2523, 2527, 2529, 2534, 23359, 12902, SMC 1659) and from Gozal Darreh Post, central upper Lar valley at an altitude of 2 600 m (ZIG). Thirty-six specimens.

Some specimens were studied during a later stage of the work and are included to some extent in the descriptions and morphological examinations, but were not included in the statistical analyses. These specimens include four *V. xanthina* from Ak Dagh, north of Alanya, south Turkey (Hans Triet collection), the two types of *V. xanthina* (BM), a topotype of *raddei* (BM), three more Mt. Hermon *bornmuelleri* and several additional *xanthina* from Ciglikara (ZIG) and from Selcuk-Ephesus (Herbert Billing collection and Bern Zoo).

STATISTICAL TECHNIQUES

Simple statistics were performed using the Statistical Analyses System (see SAS Users' Guide: Statistics 1982). Standard errors accompanying mean character ratios were used as a relative measurement of dispersion; no statistical significance is implied.

Centroid Hierarchical Cluster Analysis and Canonical Discriminant Analysis (the Candisc procedure) were utilized with the help of SAS at Gothenburg University Computer Center (GUC) (see Sneath and Sokal 1973 for review of the procedures).

The Centroid Cluster Analysis was performed using the Cluster and Tree procedures and considering both "number of clusters" and "distance between centroids". Population means for 27 variables were used, based on geographical samples with males and females treated separately.

The Canonical Discriminant Analysis, like the Cluster Analysis, is used to determine whether there are demonstrable morphological differences among the geographical groups analysed. The groups are ordinated so that they show minimum overlap (maximum separation), and in this way aggregations of phenetically similar samples are illustrated, allowing an interpretation of population affinities (Sneath and Sokal 1973).

The principal results of the discriminant analysis were generated at GUC, and the results of the analysis (on file at GUC) indicated that the specimens examined fell well within the appropriate taxa recognized earlier (Nilson and Andrén 1984 b, 1985 a, 1985 b) and in the present study.

For the purposes of this paper, if the canonical discriminant analysis demonstrates that the taxonomic units are morphologically distinct, no further explanation is required. If the canonical and the cluster analyses only partly separate the studied populations, then other data are added when available, or characters are analysed separately, to see if the additional information supports the taxonomic groupings as originally determined.

The useful outputs of the canonical discriminant analyses as used herein are the plots of the first two discriminant axes, but the third axis also gives some information on morphological distinctiveness. The plots give a visual presentation of the distinctiveness, and it is this feature that is used to demonstrate the relative morphological separation of the groups analysed. A geographical sample would have to be clearly distinctive to warrant taxonomic recognition.

ANALYSIS OF MORPHOLOGICAL CHARACTERS

The different external morphological characters vary in different aspects within the complex. Many characters are rather constant, while others vary either in a clinal fashion or with marked gaps. The clinal variation can be seen both within formal taxa and between them. This is also true in some cases with the morphological gaps. The taxonomic considerations of this variation will be discussed in the next section, where a more full consideration will be made of the total variation of all characters together. In this part we will first discuss the different external characters one by one, with an evaluation of plesiomorphic and apomorphic states. To satisfy the requirements of a character state being derived, we follow the criteria stated by Marx & Rabb (1970, 1972). The smaller European vipers of the *berus* and *aspis* groups are here treated as less advanced, since the *xanthina* — *lebetina* stem is a continuation of the same stem that split off the smaller vipers (Groombridge 1980). In the most characters, the advanced vipers of the Middle East (*xanthina* and allies) are continuations of the developmental patterns found in the smaller European vipers. Thus, character states commonly found in these last groups are considered as plesiomorphic when occurring in the *xanthina* complex. Comparison data are mainly from Saint Girons (1978) but some comparative information is also from Marx & Rabb (1972).

Size:

As a rule the male seems to be the larger of the two sexes. In the western *V. xanthina* several males reach well above 90 cm total length, with the largest one measuring 96.0 cm. All the females, except one, measure around 70 cm or less. A single female in our material (from Xanthos) measures 96.1 cm. It is a well-fed captive-born specimen, and is perhaps not representative of the situation in nature. Anyhow, physiologically both sexes seem to be able to reach this size. There seems to be little geographical or altitudinal variation in this characteristic. A male from Canakkale at the western side of the Dardanelles measured 88.0 cm, another male from an inland locality close to Ankara measured 74.0 cm, one male from the Sultan Dag mountains was 90.0 cm, and one male from the Greek island of Patmos was 71.5 cm. Males from southern lowland localities such as Xanthos and Antalya, as well as from the high altitude locality Ciglikara, measured 96.0 cm. The assumption that inland *xanthina* grow larger than coastal ones (Trutnau 1981) could not be verified. Neither could numerous quotations in the literature of sizes up to 150 cm for Turkish *xanthina* be confirmed.

In taxa further eastward from the range of *V. xanthina* the size seems to vary between different more or less isolated populations. This may reflect the real situation, but may also in some cases be a result of too small samples. The only known female of *V. bulgardaghica* in Cilician Taurus is 42.0 cm, while the two males are 48.1 and 59.1 cm. This is, however, in accordance with the western (Mt. Liban) populations of *V. bornmuelleri*, where the largest male measures 53.8 cm and the largest female 47.3 cm. The eastern *V. bornmuelleri* population (Mt. Hermon) grows bigger with both males and females around 60 cm. Maximum size in this population is from a female in captivity (ZIG) which measured 75.6 cm.

Of the more eastern taxa, nothing can be said about *V. wagneri* with a single specimen known, a juvenile female of 29.1 cm length. Of *V. raddei* the largest specimen, a male from Ara-Iler in the USSR, measures 99.2 cm, but specimens from Digor and Mt. Ararat in eastern Turkey and from Khoi in north-western Iran also reach sizes of around 90 cm. The females are slightly smaller, reaching almost 80 cm in total length in the different populations. The largest female is 79.0 cm. Again there seems to be a decrease in size towards the east. The largest male of *V. albicornuta* is 66.0 cm, but here again only three specimens have been examined. Males of *V. latifii* from the Lar valley in northern Iran reach 78.0 cm, while the largest female is 70.0 cm in total length. In spite of the high number of *raddei* investigated ($n = 72$), no specimen longer than 100 cm was found. The statement by Mertens (1967) that specimens between 100 and 110 cm "nichts Ungewöhnliches sind" could not be verified. Joger (1984) gives a maximum length of 80 cm for this species, which is a more realistic measurement.

Relative length of tail: (Table 1)

The high number of ventral plates in the eastern *raddei* group is not followed by a higher number of subcaudals, and the normally slender snakes in this eastern group have a short tail. This is most pronounced in the different populations of *raddei*, while *V. albicornuta* and *V. latifii* have a higher subcaudal count and relatively longer tails. The Lar valley population of *V. latifii* is, however, rather polymorphic in this respect. The westernmost populations of the *xanthina* species-group have a higher relative length of tail, and a clear clinal pattern cannot be found in males. Males of *Vipera bornmuelleri* and the single *V. wagneri*, which all have few subcaudals, have a tail of the same relative size as *V. xanthina* and *V. bulgardaghica*. This is probably due to the stout body shape that is found in *V. bornmuelleri*. Short relative length of tail is regarded as a derived character state.

Ventrals: (Fig. 2—3)

The number of ventral plates shows a pronounced clinal pattern, both amongst the western *xanthina* species-group and the eastern *raddei* and related taxa, with the highest numbers in western populations and a decrease towards the east. There is, however, not a uniform clinal decrease but, especially in the western assemblage of taxa, a stepwise decrease with clear gaps in between. These gaps are to some extent confined to the borders between nominal taxa, but do also occur within taxa. The

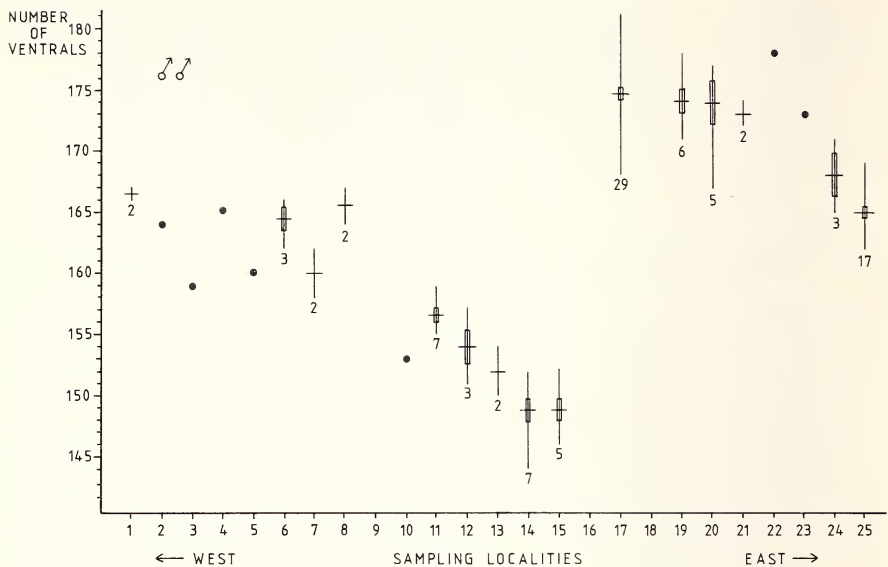


Fig. 2: Number of ventrals in males, given as mean, range, and standard error (when three or more specimens are available).

north and northwestern Anatolian populations of *V. xanthina* have a rather high ventral count. This is abruptly reduced when it comes to south Anatolian populations (Fig. 2—3). The separation line between these populations runs in an east-west line (Fig. 29) and the southern and northern *xanthina* are, in most parts along this line, separated by a region where no populations have been discovered so far. The mean value for the northern group is about eight ventrals higher than for the southern group in both sexes, and this is true for all examined local populations. However, there seem to be intermediate groups in the westernmost and easternmost parts of the separation line. In the Aegean Sea, on the islands of Patmos and Lipsos, a partly intermediate group occurs (compare Fig. 2); and in the east, at Ak Dagħ north of Alanya in the Taurus mountains, a similar intermediate population occurs with the ventral count of 157.3, as mean value for three males (only partly damaged moulted skins and photographs of living specimens have been available and this population is only included in the analyses when so stated).

The ventral count is less in *V. bulgardaghica* and has its lowest level in *V. bornmuelleri*. The two *bornmuelleri* populations (Mt. Liban and Mt. Hermon) which otherwise are different in many characters, are equal in number of ventrals and form a lowest plateau for this characteristic in the whole complex. Further east, *V. wagneri* is back to the same number of ventrals as in the western populations of *xanthina* and connects the former group of taxa with the eastern *raddei*-related forms. This latter group has higher ventral numbers than its western relatives. *Vipera raddei* has the highest numbers,

but also within this taxon a weak cline has been developed where the USSR populations have the highest numbers, followed by the Turkish populations and ending with the northwest Iranian ones as perhaps lowest. *Vipera albicornuta* has a further reduced number of ventrals, and the lowest number in this eastern assemblage of taxa is found in *V. latifii* in northern Iran (Fig. 2—3).

The western taxa never reach the high numbers of the eastern ones. Meanwhile there seems to be a selection for an increased number of ventrals with increase in body size, while no reduction of ventrals during selection for smaller size seems to occur in *Vipera*, as pointed out by Saint Girons (1978) for *Vipera latasti monticola*. Therefore we consider the low number of ventrals in *bornmuelleri* and *bulgardaghica* as a symplesiomorphy. A high number of ventrals is a synapomorphy in the *raddei* species-group as well as for the northern populations of *xanthina* and for *wagneri*. The evolution of a high number of ventrals in the northern *xanthina* populations may have occurred concordantly with the *raddei* species-group, as *xanthina* seems to be in a process of differentiation and the high ventral count is only found in some (the northern) populations which also are recent invaders of the present range, as discussed later. A similar high ventral count is also reached in the eastern *wagneri* and in the *raddei* group, and this pattern may either have been reached by parallel evolution in the two groups or it may indicate a clear phylogenetic line towards a higher number of ventral plates. High ventral count is regarded as a derived character state.

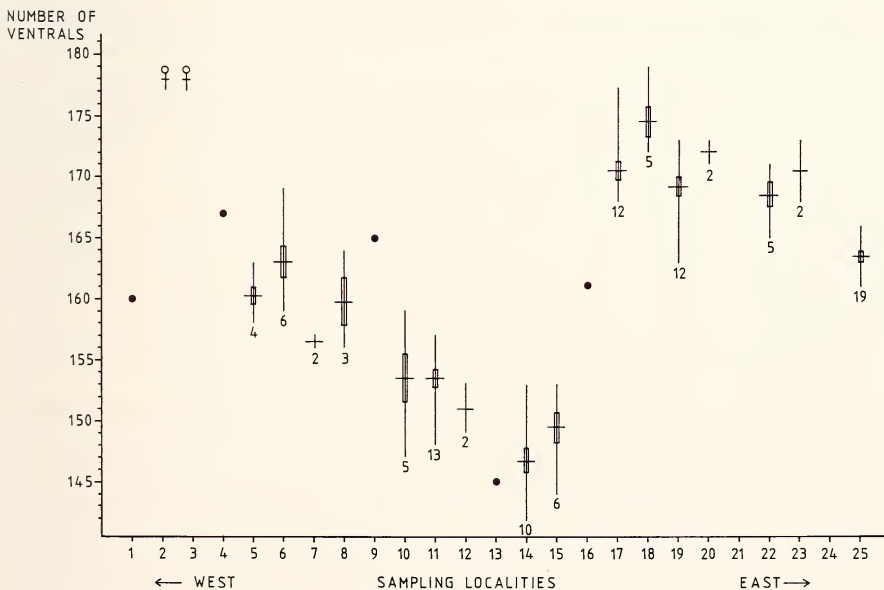


Fig. 3: Number of ventrals in females, given as mean, range, and standard error (when three or more specimens are available).

Preventrals:

The number of preventrals is rather constantly two in most populations. The only exceptions are northern *raddei* which have a mean value of three, and southern *raddei* which have 2.9. The single *V. wagneri* also has three. *Vipera albicornuta* have 2.3 and *latifii* 2.1. *Vipera xanthina* and related populations in the west all have mean values between 1.9 and 2.0. Three preventrals is considered as a derived character state.

Subcaudals: (Table 1)

The number of subcaudals varies much between different taxa and groups of populations, and most populations have a high variation in this character. This variation is most pronounced in *V. latifii*. As in the number of ventrals, there is a clinal variation also in subcaudals in the western group of taxa, with the lowest value in *bornmuelleri* and *wagneri*, and with a continuous increase through *bulgardaghica*, southern and northern *xanthina*, the highest numbers being in the latter's northern populations.

In the eastern group there is a reversed pattern to that in the number of ventrals. The number of subcaudals is lowest in the different *raddei* populations, with a marked increase in male *latifii* and *albicornuta*. There seems to be little variation between the different *raddei* populations examined, and the relatively low number of subcaudals in this taxon in relation to the high number of ventrals is reflected in the relatively short tail. Thus three different groups of subcaudal numbers can be established: one with

T a b l e 1 : Subcaudals and relative tail length (in % of total length) in adults, given as mean, standard error, and number of specimens (in parentheses).

	Subcaudals		Relative tail length	
	Males	Females	Males	Females
north <i>xanthina</i>	34.3 ± 0.5 (14)	31.2 ± 0.5 (17)	9.4 ± 0.3 (9)	9.6 ± 0.3 (10)
south <i>xanthina</i>	32.1 ± 0.5 (11)	29.8 ± 0.4 (19)	9.2 ± 0.9 (3)	9.8 ± 0.3 (9)
<i>bulgardaghica</i>	31 (2)	26 (1)	8.7 (2)	10.2 (1)
Mt. Liban <i>bornmuelleri</i>	29.5 ± 0.4 (11)	25.6 ± 0.6 (10)	9.6 ± 0.2 (8)	8.7 ± 0.3 (11)
Mt. Hermon <i>bornmuelleri</i>	28.8 ± 0.5 (4)	25.6 ± 0.4 (5)	9.6 (1)	8.2 (2)
<i>wagneri</i>	—	24 (1)	—	7.2 (1, juv.)
north <i>raddei</i>	31.9 ± 0.2 (43)	30.0 ± 0.2 (31)	7.0 ± 0.1 (38)	6.9 ± 0.1 (23)
south <i>raddei</i>	32.5 (2)	29.4 ± 0.7 (5)	6.7 (2)	7.1 ± 0.1 (5)
<i>albicornuta</i>	36.0 ± 1.0 (3)	—	8.7 ± 0.3 (3)	—
<i>latifii</i>	34.3 ± 0.5 (16)	29.7 ± 0.5 (17)	8.8 ± 0.5 (6)	7.9 ± 0.4 (8)

very low subcaudal count (*bornmuelleri*, *bulgardaghica*, *wagneri*), one large assembly of populations with a moderate number (*raddei*, *xanthina*), and one with an increasing number of subcaudals (*albicornuta*, *latifii*). We consider this as a unidirectional evolutionary character path containing three states and evolving in a direction towards higher number of subcaudals. We consider moderate and high numbers of subcaudals as subsequent derived character states.

Dorsal scale rows:

The number of longitudinal scale rows on body also varies to some extent in different populations. On the anterior part of the body, the lowest numbers are found in the west (north *xanthina*: $\bar{x} = 22.95 \pm 0.1$) and in the east (*latifii*: $\bar{x} = 22.7 \pm 0.2$). The geographically intermediate populations all have higher numbers. In the south *xanthina* populations, the number is increased to 23.7 ± 0.2 , and in *bulgardaghica* to 24.3 ± 0.6 ; *bornmuelleri* has 23.3 ± 0.2 , *wagneri* has 25, each of the different *raddei* populations has 23.4 ± 0.1 – 0.2 , and a slight decrease appears in *albicornuta* to 23.0 before reaching the low value of *latifii*. This last population is the most polymorphic in this character, ranging from 17 to 25 scales on the neck.

With the exception of the western populations (Mt. Liban) of *bornmuelleri*, all different populations seem to have 23 scale rows on the midbody. Rare exceptions with 25 midbody scale rows are found in northern *xanthina* (Izmir, Aegean Sea, Denizli), in *bulgardaghica*, and in the Ara-Iler and Khoy populations of *raddei*. Besides *bornmuelleri*, 21 scale rows are found in a single Ara-Iler *raddei* and in four *latifii*. Eight (= 42 %) of the Mt. Liban *bornmuelleri* have 21 scale rows, while all the Mt. Hermon specimens of *bornmuelleri* have 23.

On the posterior part of the body, the number is rather constant around 17 scale rows in most taxa. Again, only in the Mt. Liban population of *bornmuelleri* is the number less in half of the specimens. In the Mt. Hermon population of the same taxon, the number is 17, or even 19 in one specimen. Most specimens of *raddei* have 17 scale rows, but in all examined populations there are also a few individuals with 18 or 19 scale rows. Mean for the northern *raddei* is 17.5 ± 0.1 . In the southern *raddei* populations in Iran, more than half of the specimens have a higher number than 17 scale rows on the posterior part of body. Mean for the southern *raddei* form is 18.1 ± 0.3 . *Vipera latifii* also show some variation with values ranging from 16 to 18 ($\bar{x} = 17.0 \pm 0.1$).

The normal number of 23 midbody scale rows is intermediate between the situation in the smaller European vipers with 19–21 rows and larger Oriental vipers (*palaestinae* — *lebetina* and allies) with 25–27 midbody scale rows. Thus, 23 scale rows is a synapomorphic character state for the entire *xanthina* complex. The low number of 21 found in Mt. Liban populations of *bornmuelleri* has probably evolved secondarily due to selection for small size, and this is considered as an apomorphic state. A similar situation is found in the dwarf viper, *Vipera latasti monticola*, as discussed by Saint Girons (1978). With a parallel argumentation, a tendency towards fewer posterior scale rows is considered as a derived character state.

Supraocular position and shape:

The position of the supraoculars falls into two clear different states. Either they are in broad contact with the eyes or they are separated from the eyes by circumocular scales. In the latter case the circumocular ring is completely surrounding the eye. The mainly western species *xanthina*, *bulgardaghica*, *bornmuelleri*, and *wagneri* all fall into the former category while *raddei*, *albicornuta*, and *latifii* belong to the latter.

The position of circumocular scales between the eye and the supraocular plate causes a slightly raised position of the latter, giving an appearance of a weak horn above the eye. Similar raised eyebrows can also be seen in *xanthina* and *bornmuelleri* but are never as pronounced. The "horn effect" is further pronounced by the fact that the outer border of the supraocular plate is strongly bent into a right angle in *raddei*, *albicornuta*, and *latifii*. The corresponding outer border of supraoculars in *xanthina*, *bulgardaghica*, *bornmuelleri*, and *wagneri* is straight.

The conditions with a complete inner circumocular ring that separates the supraocular from the eye, and where the outer border of the supraocular is projecting in a right angle, are unique characters within *Vipera* and here considered as derived character states.

T a b l e 2 : Number of some scale characteristics given as mean, standard error, and number of specimens (in parentheses).

	Apicalia	Second chinshields	Subocular* rows
north <i>xanthina</i>	2.13 ± 0.1 (22)	4.17 ± 0.1 (24)	3.96 ± 0.03 (26)
south <i>xanthina</i>	2.00 ± 0.0 (28)	4.22 ± 0.1 (27)	4.00 ± 0.00 (27)
<i>bulgardaghica</i>	2.67 ± 0.3 (3)	4.00 ± 0.0 (3)	2.67 ± 0.33 (3)
Mt. Liban <i>bornmuelleri</i>	2.56 ± 0.1 (18)	5.20 ± 0.2 (15)	4.05 ± 0.05 (19)
Mt. Hermon <i>bornmuelleri</i>	2.55 ± 0.2 (9)	4.00 ± 0.0 (8)	4.00 ± 0.0 (9)
<i>wagneri</i>	2 (1)	4 (1)	4 (1)
north <i>raddei</i>	2.38 ± 0.1 (72)	4.19 ± 0.1 (73)	4.00 ± 0.00 (74)
south <i>raddei</i>	2.11 ± 0.1 (9)	4.11 ± 0.1 (9)	4.00 ± 0.00 (9)
<i>albicornuta</i>	2.00 ± 0.0 (3)	4.00 ± 0.0 (3)	3.33 ± 0.67 (3)
<i>latifii</i>	2.61 ± 0.1 (36)	4.5 ± 0.10 (36)	3.81 ± 0.09 (36)

* Sum of left and right sides

Apicals: (Table 2)

The number of apicals in contact with the rostral is either two or three. There seems to be little variation between populations within nominal taxa. In *xanthina* two apicals is the most common situation. Only three specimens (6 %) had three apicals instead of two. In *bulgardaghica* and *bornmuelleri* both states occur, but here three apicals is dominating (in 66 and 73 % respectively). Also in *raddei* the "two apicals" state is dominating, but three apicals in contact with the rostral is a common occurrence. Between 28 and 50 % of the snakes in the local populations can be in this last state. Altogether for the norther *raddei*, 35 % have three apicals. In the southern populations in Iran, this state seems to be rare. Only one (11 %) of the examined specimens had three apicals. In *albicornuta* only two apicals have been observed, while in *latifii* three apicals seems to be the rule. This is also in line with the situation amongst the smaller European vipers, with one apical in *ursinii* and two in *berus* and *aspis*, with a tendency towards three in the latter. Thus the tendency towards three apicals is considered as a derived character state in the *xanthina* complex. It seems to have evolved through parallelism in different populations.

Circumoculars: (Table 3)

The mean number of scales in the inner circumocular ring varies in an undulating fashion from the western *xanthina* populations to the eastern *V. latifii*. Within taxa, there seems to be comparatively little variation. The lowest value is found in *bulgardaghica* while the mean number increases again through *bornmuelleri* and *wagneri*, with the highest mean numbers in *raddei*. Then there is again a decrease through *albicornuta* to *latifii*, which again has a rather low value. The distal second circumocular ring shows little variation through all the different populations except *bulgardaghica*, which has extremely low numbers. High numbers of scales in the first and second circumocular rings are considered as derived character states, which is in line with the situation amongst the smaller European vipers, where it ranges from around eight in *ursinii* to eleven scales in *ammodytes* in the inner circumocular ring on each side of the head.

Supralabials: (Table 3)

In *xanthina* ten supralabial plates on each side is the normal state, while nine is the rule in the remaining taxa. Some variation occurs, however, and in the northern *xanthina* all combinations from nine to eleven supralabials can be found. Also, *raddei* can rarely have ten supralabials on each side, but most variable is *latifii* which can have as many as twelve supralabials on both sides. Ten supralabials is, however, the rare state in this complex of vipers, and is considered as a derived character state. This is in agreement with Marx & Rabb (1972) who considered a general increase of supralabials in Colubroidea as an apomorphic event.

Sublabials: (Table 3)

The number of sublabial plates shows much variation in all populations, but with

Table 3 : Number of head scales given as mean, standard error and number of specimens (in parentheses).

	1:st circumoculars*	2:nd circumoculars*	Supralabials*	Sublabials*
north <i>xanthina</i>	24.5 ± 0.3 (26)	29.0 ± 0.4 (19)	19.9 ± 0.1 (26)	25.1 ± 0.4 (26)
south <i>xanthina</i>	24.2 ± 0.3 (30)	29.8 ± 0.4 (23)	19.7 ± 0.2 (29)	25.0 ± 0.4 (27)
<i>bulgardaghica</i>	20.0 ± 0.6 (3)	22.3 ± 1.3 (3)	18.0 ± 0.0 (3)	23.0 ± 0.6 (3)
Mt. Liban <i>bornmuelleri</i>	24.6 ± 0.5 (19)	28.8 ± 0.5 (19)	18.2 ± 0.1 (14)	24.1 ± 0.3 (15)
Mt. Hermon <i>bornmuelleri</i>	24.1 ± 0.5 (11)	30.4 ± 0.3 (11)	18.4 ± 0.2 (10)	23.6 ± 0.3 (8)
<i>wagneri</i>	29 (1)	30 (1)	18 (1)	25 (1)
north <i>raddei</i>	29.1 ± 0.3 (74)	30.5 ± 0.2 (73)	18.2 ± 0.01 (73)	23.9 ± 0.1 (71)
south <i>raddei</i>	29.1 ± 0.9 (9)	30.4 ± 0.4 (9)	18.0 ± 0.0 (9)	23.1 ± 0.4 (9)
<i>albicornuta</i>	27.3 ± 0.7 (3)	29.0 ± 2.1 (3)	18.0 ± 0.0 (3)	23.3 ± 0.7 (3)
<i>latifii</i>	25.4 ± 0.4 (36)	28.2 ± 0.2 (34)	18.6 ± 0.2 (36)	23.4 ± 0.3 (36)

* Sum of left and right sides

higher numbers in the different *xanthina* populations. The number ranges from 11 to 14 on each side in most *xanthina* populations but one specimen from Ciglikara had only 8/9 sublabials. *Vipera bornmuelleri*, north *raddei* and *latifii* normally have between 11 and 13 sublabials, while *bulgardaghica* and south *raddei* have 12 as an upper limit. *Vipera latifii* can also have as few as 9 sublabials. A high number of sublabials is generally considered as a synapomorphic character state.

Second chinshields: (Table 2)

The normal situation is four chinshields in a transverse row behind the first pair of chinshields. Single specimens with five chinshields can be seen in *xanthina* and *raddei* populations. The most divergent population is the western (Mt. Liban) *bornmuelleri*, where most specimens (67 %) have more than four second chinshields. Six chinshields seems to be the most frequent state in this population, while the eastern *bornmuelleri* (Mt. Hermon) in all examined cases only have four shields. Also *latifii* shows great polymorphism in this character, as 31 % of the examined snakes have more than four chinshields. This species frequently has as many as seven second chinshields. The tendency towards more than four chinshields is considered a derived character state. The similarity between *latifii* and western *bornmuelleri* is an example of parallel evolution in small populations.

Interocular rows: (Table 4)

The numbers of interocular rows between the supraoculars varies between six and nine in most taxa, with the exception of *bulgardaghica* and *wagneri* where only six rows are found, and of *albicornuta* with only seven. This last figure is also the lower border for *latifii*. *Vipera xanthina* only rarely reaches nine scales, while this is more common in all *raddei* populations (see Table 4 for mean values). The most divergent patterns are found in the *bornmuelleri* populations. All the snakes from the western (Mt. Liban) populations have six to eight rows ($\bar{x} = 7.15 \pm 0.18$) while all the eastern (Mt. Hermon) specimens have eight to nine rows ($\bar{x} = 8.36 \pm 0.15$). This character is not alone included in the phylogenetic analysis due to the great variation in all taxa (see below).

T a b l e 4 : Number of head scales given as mean, standard error, and number of specimens (in parentheses).

	Canthals*	Scales in interocular row	Intercanthals	Inter- supraoculars
north <i>xanthina</i>	2.0 ± 0.0 (20)	6.6 ± 0.2 (27)	10.7 ± 0.4 (20)	30.8 ± 1.1 (20)
south <i>xanthina</i>	2.1 ± 0.1 (23)	6.9 ± 0.1 (30)	11.4 ± 0.3 (22)	30.9 ± 0.8 (22)
<i>bulgardaghica</i>	2.0 ± 0.0 (3)	6.0 ± 0.0 (3)	10.7 ± 1.5 (3)	30.0 ± 3.5 (3)
Mt. Liban <i>bornmuelleri</i>	2.6 ± 0.2 (14)	7.1 ± 0.2 (19)	13.9 ± 0.5 (14)	34.9 ± 0.8 (14)
Mt. Hermon <i>bornmuelleri</i>	2.7 ± 0.1 (9)	8.3 ± 0.2 (12)	15.7 ± 0.9 (9)	36.5 ± 1.1 (12)
<i>wagneri</i>	2 (1)	6 (1)	14 (1)	29 (1)
north <i>raddei</i>	4.2 ± 0.1 (73)	7.4 ± 0.1 (74)	14.9 ± 0.3 (73)	29.2 ± 0.4 (74)
south <i>raddei</i>	3.8 ± 0.2 (9)	7.6 ± 0.3 (9)	14.0 ± 0.7 (9)	27.6 ± 2.0 (9)
<i>albicornuta</i>	4.0 ± 0.0 (3)	7.0 ± 0.0 (3)	13.3 ± 1.3 (3)	26.3 ± 1.2 (3)
<i>latifii</i>	4.2 ± 0.1 (33)	7.4 ± 0.1 (34)	14.7 ± 0.4 (34)	26.9 ± 0.6 (34)

* Sum of left and right sides

Intersupraocular scales: (Table 4)

The number of intersupraocular scales also shows great variation within all examined populations, but no differences between populations within the different species could be detected. The southern *raddei* populations in Iran show the greatest variation, with values ranging from 18 to 37 intersupraocular scales. The *bornmuelleri* populations have the highest values with an upper limit of 42 scales (see Table 4 for mean values).

Intercanthal scales: (Table 4)

The intercanthals also show some variation within the local populations, but there is little differentiation between populations in nominal taxa. Again, the only exception seems to be *bornmuelleri* where the Mt. Liban population has a mean value of 13.85 ± 0.52 SE, while the Mt. Hermon population has 15.27 ± 0.78 SE. Populations of *V. xanthina* and *V. bulgardaghica* have lower values than the remaining taxa.

Crown scales (Intersupraoculars + Intercanthals):

All the intersupraoculars and intercanthals taken together show a similar pattern as in each of the two groups. No marked variation between populations of true species can be seen except in *bornmuelleri*, which also has the highest numbers. The eastern Mt. Hermon population has a mean value of 51.9 ± 1.6 SE scales, while the western Mt. Liban populations have a mean value of 49.6 ± 0.9 SE scales. A higher fragmentation of crown scales (intersupraoculars + intercanthals) is considered as a derived character state.

Subocular rows: (Table 2)

The normal state is two subocular rows on each side, and this is the dominating state in all populations except in *bulgardaghica*, where all three available specimens have a single subocular scale on one side of the head or both. Of the remaining taxa, a single northern *xanthina* from Canakkale had a single scale on one side of the head. One *albicornuta* and two *latifii* had single scales on both sides of the head, and one *bornmuelleri* from Mt. Liban had three scales on one side of the head. A condition with a single subocular row is considered as a plesiomorphic character state; thus two scale rows is a synapomorphy within the *xanthina* complex.

Canthals: (Table 4)

The number of canthal scales is basically one on each side of the head in the western assembly of taxa (*xanthina*, *bulgardaghica*, *bornmuelleri*, and *wagneri*) while two scales on each side of the head is usual in the remaining eastern species (*raddei*, *albicornuta*, and *latifii*). In *bornmuelleri*, a loreal scale penetrates somewhat in between the canthal and the supraocular in some specimens, raising the number to one and a half scales on each side. This is most pronounced in the eastern Mt. Hermon populations, where a single specimen with two canthals on each side was also found. Four specimens of the southern *xanthina* also have one and a half canthals on each side. The different *raddei* populations all have values normally ranging from two to two and a half canthal scales on each side. Three specimens from Digor in Turkey had three canthals on each side. Rarely, fewer canthals can occur in *raddei*. One specimen, also from Digor, and one southern *raddei* from Khoi in Iran had one and a half canthals on each side. Again, *latifii* shows a marked polymorphism in this character. It varies from one and a half to three and a half canthals on each side of the head. An increased number of canthals is considered as a derived character state.

Size of upper preocular:

Some taxa such as the *raddei* group, *bornmuelleri*, and *bulgardaghica* have a more or less elongated upper preocular, while others like *xanthina* and *wagneri* have more rounded ones. In *bulgardaghica* it is very long, reaching the nasal or nearly so. In all the other populations, the upper preocular is separated from the nasal by a loreal scale. In two cases, one *xanthina* from Sultan Dagħ, Turkey and one *raddei* from Ara-Iler, USSR, the preocular was fused with the loreal, thus forming a long scale that stretched between eye and nasal. An elongated upper preocular that reaches the nasal or nearly so is considered as a plesiomorphic character state, while a shorter preocular, separated from the nasal by a loreal, is a derived state. This is a parallel situation to that in the smaller European vipers, where *ursinii* and some *berus* have the long upper preocular and the remaining taxa normally have a shorter one.

Neck pattern:

The pattern on the posterior part of the head normally consists of two oblique separate bands that approach anteriorly without meeting. This state is found in all taxa and populations, and is the only one found in the rare species *bulgardaghica*, *wagneri*, and *albicornuta*. In two population groups, *latifii* and southern *raddei*, these neck bands can be totally missing. Otherwise, *latifii* is also characterized by having the normal state. The two bands can also in some cases be transverse to the body axis, and this is specially pronounced in *raddei*, especially in Digor and to some extent in the Ara-Iler populations. To a varying degree, one or both of the neck bands are also united with the dorsal zig-zag band, forming a lyre pattern on the nape. This occurs infrequently in all the different *raddei* populations as well as in western (Mt. Liban) *bornmuelleri* although more rarely. This kind of neck pattern is also a rule (56 %) in the southern *xanthina*, while occurring less often (25 %) in the northern populations of the same species. Due to the great variation, this character has not been included in the phylogenetic analysis.

Dorsal pattern: (Fig. 4—7)

The number of blotches or windings in the dorsal pattern differs markedly between different taxa, but also to some extent within certain taxa (Fig. 4). The northern populations of *xanthina* vary between 26 and 42 ($\bar{x} = 31.4 \pm 0.56$) while the southern *xanthina* have between 22 and 30 ($\bar{x} = 26.2 \pm 0.56$) blotches in the dorsal zig-zag band. The distinct gap in the number of blotches between the different northern populations on the one hand, and the three southern populations on the other, is a parallel case to the situation with the ventral counts in *xanthina* (see Fig. 2—3). *Vipera wagneri* with 24 blotches seems to be similar to the southern *xanthina* in this respect, but more similar to northern *xanthina* as regards the ventral count (161).

Vipera bornmuelleri, which has a pattern that can be derived from the *xanthina* type, has the highest numbers of blotches in the whole complex. Juvenile specimens of this species have a weakly developed pattern, which in shape is similar to that in juvenile

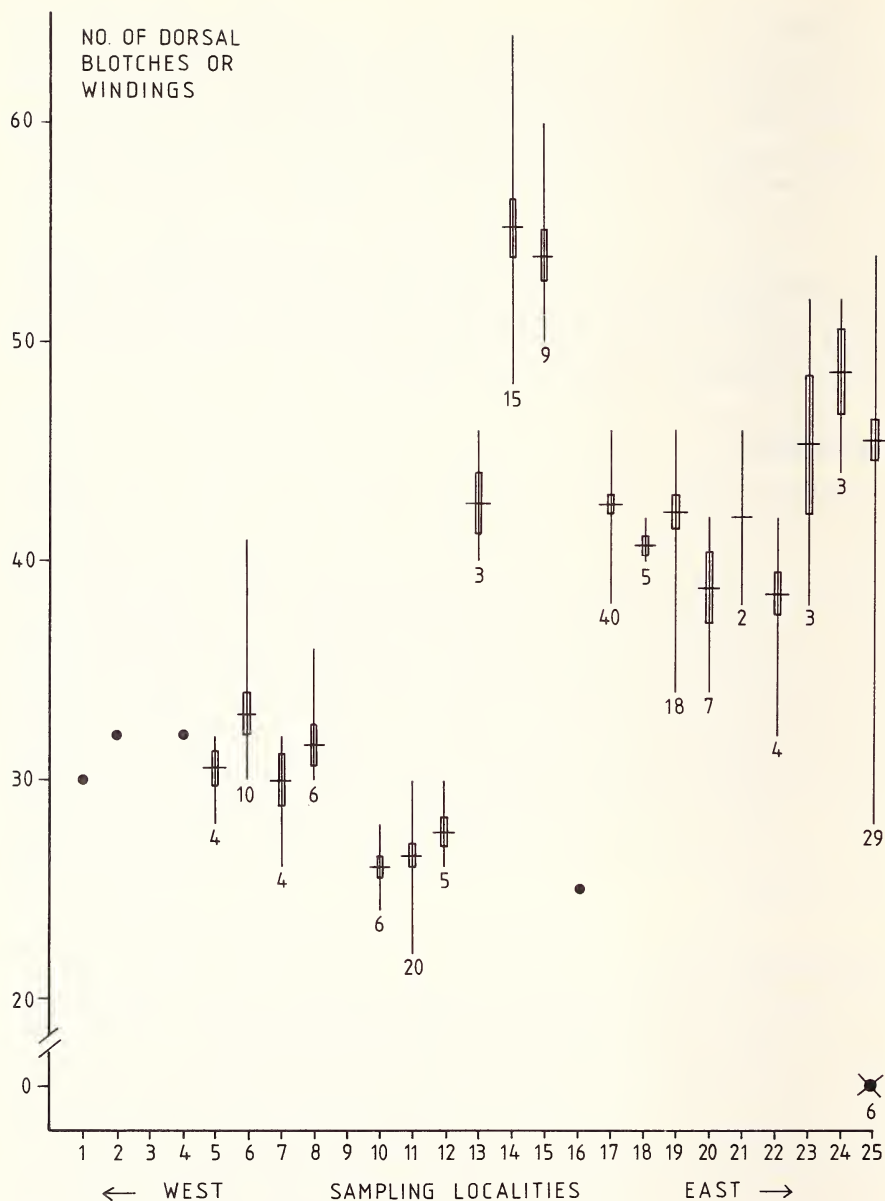


Fig. 4: Number of blotches or windings in the dorsal zig-zag band, given as mean, range, and standard error (when three or more specimens are available).

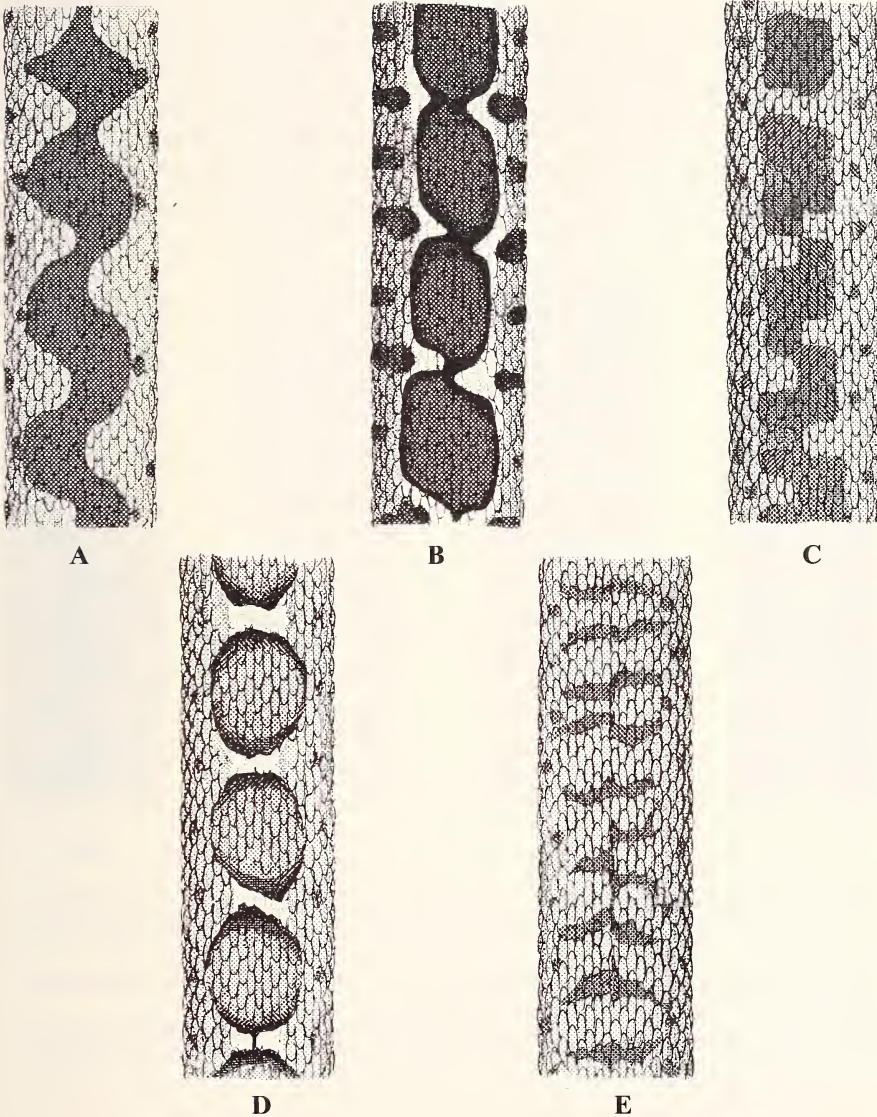


Fig. 5: Main dorsal patterns within the *Vipera xanthina* complex, based on adult specimens.
 A. *V. xanthina* (♀ from Ciglikara, SW Turkey), pattern characteristic for both sexes in southern populations and ♂ in northern populations.
 B. *V. xanthina* (♀ from Efesus, west Turkey), pattern characteristic for many northern ♀.
 C. *V. bulgardaghica* (♂ from Bulgar Dag, south central Turkey).
 D. *V. wagneri* and *V. bornmuelleri* (a ♀ *bornmuelleri* from Les Cedres, Mt. Liban, Lebanon), pattern known from ♀ *wagneri* and ♀ *bornmuelleri* from Mt. Liban.
 E. *V. bornmuelleri* (♀ from Mt. Hermon, Israel administered area), pattern characteristic for ♂ and ♀ on Mt. Hermon and for ♂ on Mt. Liban.

xanthina. But the central parts of the blotches are rather reduced and fade away almost totally with growth, leaving the darker anterior and posterior margins of each blotch. This results in an irregular, transversely banded pattern (Fig. 5 E). The numbers of these transverse bands ($\bar{x} = 54 \pm 1.0$) are also about twice the number of that found in *xanthina*. In most females in the western (Mt. Liban) population, much of the colour in the blotches remains in adult stage, resulting in similarities to females of *xanthina*, although much paler (Fig. 5 D). *Vipera bulgardaghica* is intermediate between these last two taxa in number of blotches (Fig. 5 c).

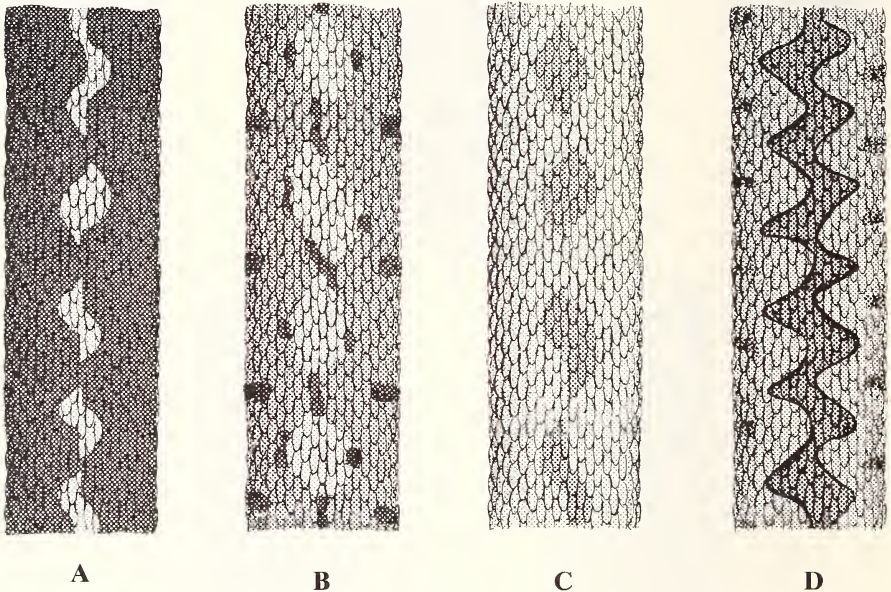


Fig. 6: Main dorsal patterns within the *Vipera xanthina* complex, based on adult specimens.
 A. *V. raddei* (♂ from Ara-Iler, north of Jerevan, USSR), pattern found in both sexes in northern populations.
 B. *V. raddei* (♀ from south of Jerevan, USSR), pattern found in both sexes mainly in northern populations but also infrequently in southern ones.
 C. *V. raddei* (♀ from Gotor, west Azarbaijan, Iran), pattern found in southern populations.
 D. *V. albicornuta* (♂ from Zanjan, Iran), pattern found, with little variation, in all specimens.

Vipera latifii is the most variable population of all in this character. Most specimens have between 38 and 54 blotches, but frequently specimens with fewer blotches can be seen. Unicoloured specimens, and specimens with a narrow vertebral line, occur frequently. Occasionally, specimens with a vertebral line having just a few irregularly detached windings occur.

Many populations show different degrees of reduced dorsal pattern. Besides *bornmuelleri*, such reductions are found in most of the eastern *raddei*-related taxa. *Vipera latifii*

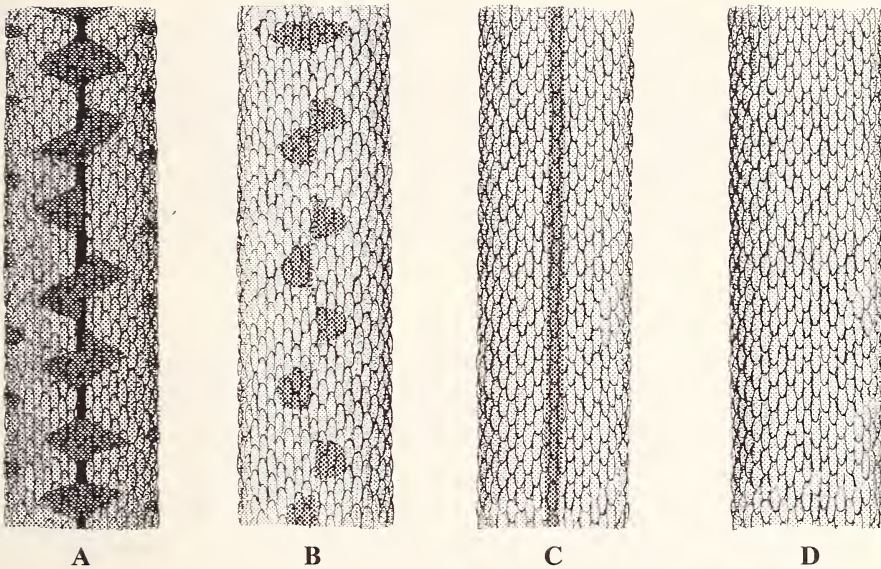


Fig. 7: Main dorsal patterns within the *Vipera xanthina* complex, based on adult specimens. A—D *V. latifii* (based on specimens from upper Lar valley, Alburz mountains, north Iran), all pattern types can occur in both sexes.

shows all trends of reductions (Fig. 7 A—D), from a developed zig-zag band, via diffuse blotches, a narrow vertebral line to an absence of pattern. Also, the dorsal blotches can be few but strongly marked, or many and very weakly coloured. *Vipera albicornuta* seems to be the only member of this eastern group of taxa that has a constant, rather pronounced dorsal zig-zag band (Fig. 6 D). *Vipera raddei* also shows different degrees of reduction in the dorsal pattern, and in this species the colour is inverted, with a darker ground colour and a lighter dorsal pattern (Fig. 6 A-B). Only in the southern populations is the typical colour pattern maintained, with specimens having a darker pattern (Fig. 6 C). But this southern population also consists of individuals with inverted pattern. Reversed or inverted dorsal colour pattern is considered as a derived character state. Also the condition with reduced dorsal markings, although parallel-evolved in different populations, is considered as a derived character state. So is doubling of rhomb numbers by divisions (in the adult stage), as in *bornmuelleri*.

ANALYSES OF POPULATION SYSTEM

Species groups

The taxa within the *xanthina* complex, even though closely related (Mertens 1952; Mertens et al. 1967; Nilson & Sundberg 1981), seem to fall into two phenetic groups, one containing the populations referred to as *raddei*, *albicornuta* and *latifii*, and the other with populations known as *xanthina*, *wagneri*, *bulgardaghica*, and *bornmuelleri* (Table 5). The obviously monophyletic *raddei* group differs from the *xanthina* group in the shape of the supraoculars (angled and raised), and in the occurrence of a complete circumocular ring that separates the supraocular from the eye (Fig. 8). They also "share a similar form of maxilla, with a narrow shaft above the main tooth-bearing portion, with a distinct medially-directed dorsal tip" (Groombridge 1980). The *raddei* species-group is also geographically more eastern than the *xanthina* group in having a Transcaucasian, east Anatolian, and a north and northwest Iranian affinity, while the *xanthina* taxa occur mainly in western and southern Anatolia, Lebanon, and the Israel-Syrian border regions (Mt. Hermon). The two species *raddei* and *xanthina* also show strong hybrid inviability if crossed (Nilson & Sundberg 1981), which indicates a long isolation allowing effective postmating isolation mechanisms to develop.

Table 5: Character comparison of the species-groups.

<i>Vipera xanthina</i> species-group	<i>Vipera raddei</i> species-group
Supraocular in broad contact with eye	Supraocular separated from eye
Inner circumocular ring not complete (interrupted by supraocular, and rarely by subocular from second distal circumocular ring [in <i>bulgardaghica</i>])	A complete inner circumocular ring
Supraocular plates not angled	Supraocular plates angled and raised
Body stout	Body slender
Less than two whole canthal scales separating supraocular and supranasal plates on each side of head	Two or more canthal scales separating supraocular and supranasal plates on each side of head
Narrow shaft above the main tooth-bearing portion of maxilla without a distinct medially-directed dorsal tip*)	Maxilla with a narrow shaft above the main tooth-bearing portion, with a distinct medially-directed dorsal tip*)
Lower ventral count (normally less than 167)	Higher ventral count (normally more than 163)
Longer tail (normally 8 % of total length or more in adults)	Shorter tail (normally 8 % of total length or less in adult females, less than 9 % in males)

*) (Groombridge 1980)

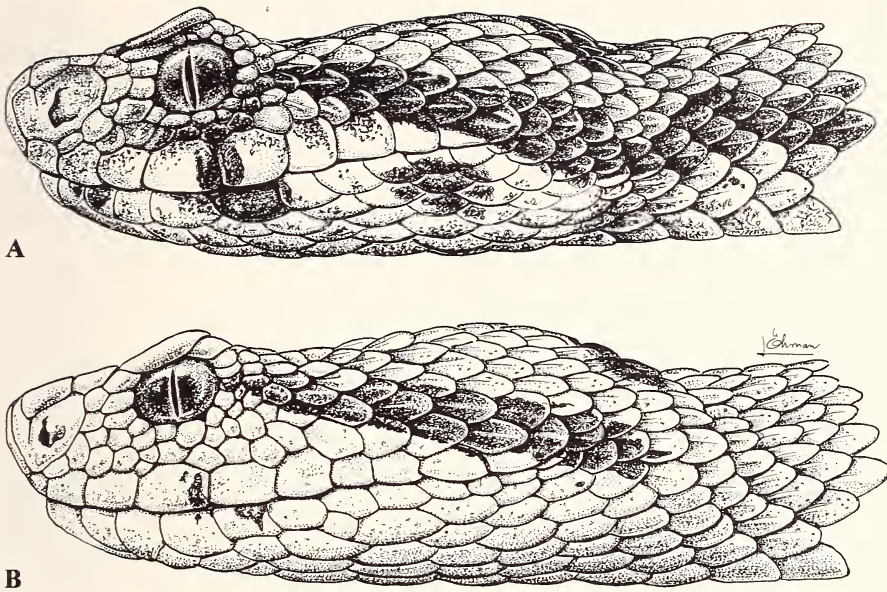


Fig. 8: Head of (A) *Vipera raddei* (based on a ♀ from Digor, province Kars, N. E. Turkey) and of (B) *Vipera xanthina* (based on a female from Ciglikara, province Antalya, S. W. Turkey), showing main differences in scalation between the *raddei* species-group and the *xanthina* species-group (compare Table 5).

Morphometric Analyses

Cluster Analyses

Cluster analysis of population mean values for all the 27 variables used shows that actually three major phenetic groups are evident in both the male (Fig. 9) and the female (Fig. 10) distance phenograms. The most distant group contains the population from Bulgar Dagħ in Cilician Taurus (*V. bulgardaghica*), followed by two major groups consisting of populations which can be referred to the *xanthina* species-group and populations of the more eastern *raddei* group, respectively. A phenetic break is evident between the latter two major groups, and the only relationship in geography between them is the small north Iranian Urmia sample (*wagneri*), which is from the region where *raddei* is also distributed.

In both groups, a number of subgroups can be found, which agrees rather well with the present taxonomic division stated earlier in this study. In the male phenogram, the *xanthina* species-group is first divided into west Anatolian and Greek populations, belonging to the true *xanthina*, and into the *bornmuelleri* populations (Bcharré and Mt. Hermon). A rather pronounced distance between the different localities can be

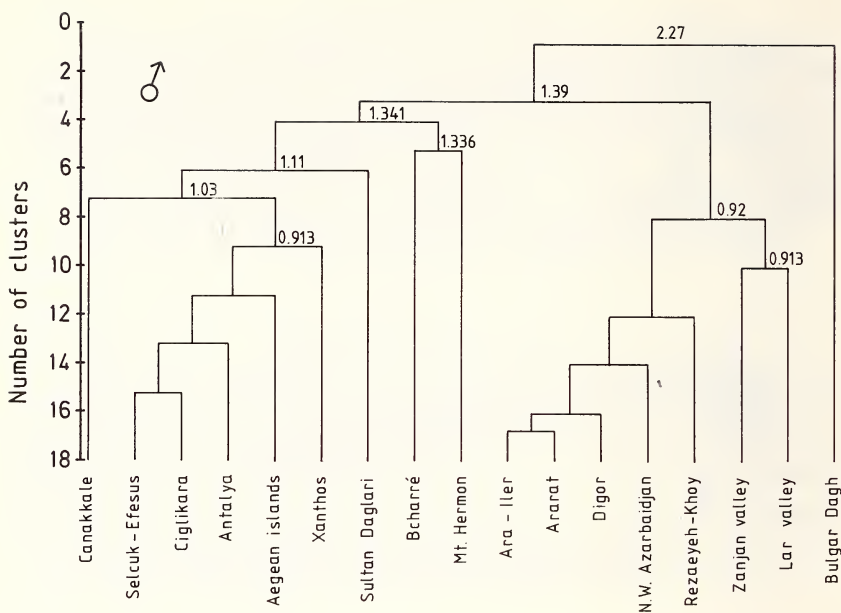


Fig. 9: Centroid Hierarchical Cluster Analysis of male specimens of the *Vipera xanthina* complex. Localities as in text and Fig. 1. Figures correspond to distance between centroids.

seen, and this is most pronounced between the two *bornmuelleri* localities, which is what can be expected concerning all the minor morphological differences as shown earlier. Rather large differences also seem to be the case between different *xanthina* populations, but they are different in the male and female analyses. Also the single specimen from Urmia (*wagneri*) is easily separated from *xanthina* at about the same level as *bornmuelleri* (Fig. 10). The Urmia population is not represented in the male analysis, as no males are known.

The large distances, different for males and females, between the local populations of *xanthina* suggest that this is a variable taxon that has undergone an evolutionary radiation in its different geographical isolates. This has been discussed earlier concerning the northern and southern populations of *xanthina*, which differ in ventral counts and in number of dorsal zig-zag windings. However, several other minor differences between local populations also exist. The coding of characters for computer analyses resulted in loss of information in some cases. As all the morphological characters used are weighted equally the differences in ventral plates and dorsal blotches are not exposed when weighted together with the rest of the characters. *Vipera xanthina* is the species that has the largest distribution and, as the species inhabits only more or less rocky habitats, the different populations are in many cases effectively isolated from other populations, and consequently they have probably been subjected to divergent micro-evolution during past times.

The different populations of *Vipera raddei* in the other group are much more closely united, and this can be expected for opposite reasons than in the discussion above. *Vipera raddei* has a much smaller distribution with densely spaced populations. For the partly rocky area of easternmost Turkey and adjacent parts of USSR and Iran, a certain gene-flow can be assumed between the different populations. The most divergent *raddei* populations are those in the Khoy and Rezaeyeh areas in west Azarbaidjan, Iran, which also are geographically the most isolated populations.

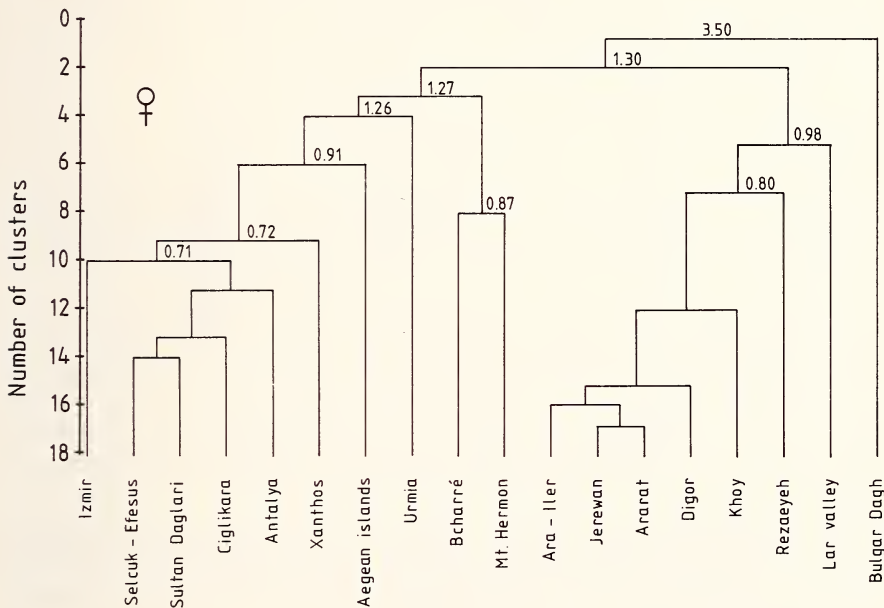


Fig. 10: Centroid Hierarchical Cluster Analysis of female specimens of the *Vipera xanthina* complex. Localities as in text and Fig. 1. Figures correspond to distances between centroids.

In the male phenogram (Fig. 9), the Zanjan populations (*albicornuta*) and the Lar valley populations (*latifii*) are separated from the *raddei* populations on the same level, indicating a similar morphological divergence and degree of separation from the *raddei* stock. The Zanjan population is not represented in the female analysis, as females were not available for this study.

No other obvious morpho-geographic correlations or discontinuities were noted in these clusters, it should be noted that some of the sample sizes on which the means were based were rather small. The level of differences between clusters and samples were about the same in both sexes, indicating that they exhibit a similar morphological variation.

Canonical Discriminant Analyses

The principal results of the first canonical discriminant analysis for the *xanthina* species-group is the discrimination of three major aggregations along the first two axes (Fig. 11). The first aggregation, to the right, represents the western Anatolian *Vipera xanthina* populations together with the Iranian *V. wagneri* (16). The middle group represents the Lebanese *V. bornmuelleri* and the third group (13), to the left, is *V. bulgardaghica*, the endemic population of the Bulgar Dagh mountains in south central Turkey.

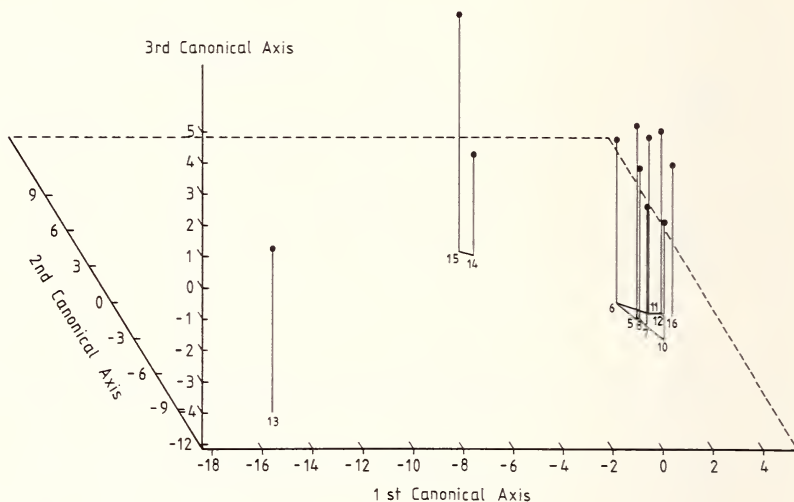


Fig. 11: Canonical Discriminant Analysis of population means of the *xanthina* species-group, showing a 3-D projection of the centroids along the first three canonical axes. Population numbers refer to Fig. 1 and the text. Populations of *Vipera xanthina* (to the right) and of *bornmuelleri* (in the middle) are connected by basal lines.

The single available Iranian specimen of *V. wagneri* is closest to the *V. xanthina* aggregation. Although widely separated geographically, the single specimen known seems to be phenetically similar, indicating a close relationship to *V. xanthina* although it shares many morphological characters with *V. bornmuelleri*.

Within the middle group of *bornmuelleri* sample means, two phenetically distinct aggregations are apparent along the third axis with one composed solely of Mt. Hermon vipers (14) and the other entirely of Mt. Liban vipers (15). This separation of the two *bornmuelleri* populations is striking but not totally unexpected, as they also are geographically isolated, restricted to high altitudes in the two mountain chains mentioned above, and separated by the deep Bekaa valley in Lebanon.

The canonical discriminant analysis of the *raddei* species-group (Fig. 12) also results in a discrimination of four major aggregations; they are, from right to left, north

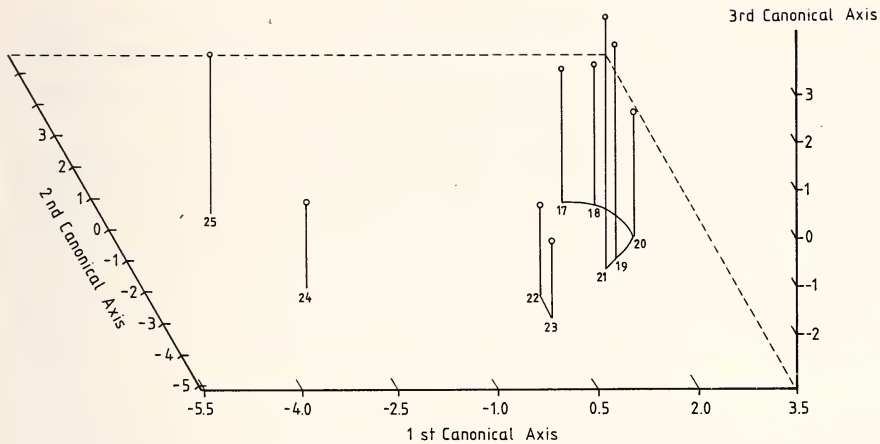


Fig. 12: Canonical Discriminant Analysis of population means of the *raddei* species-group, showing a 3-D projection of the centroids along the first three canonical axes. Population numbers refer to Fig. 1 and the text. Populations of northern and southern *raddei* respectively to the right are connected by basal lines.

raddei, south *raddei*, *albicornuta*, and *latifii*. The *raddei* aggregation is thus divided into two groups along all three axes, although less pronounced than the separation between *raddei* and the other two species. These two groups of *raddei* represent populations in two geographically separated areas. The larger group (17—21) contains populations from the USSR (17—18), northeastern Turkey (19—20), and northwestern Azarbaijan in Iran (21), while the smaller aggregation represents the southern populations from west Azarbaijan in Iran, from the Khoy area in the north (22) along the Iranian — Turkish border south to Rezaeyeh (23) (Fig. 25).

Vipera albicornuta (24) and *V. latifii* (25) are also separated from each other along all three canonical axes.

Intraspecific Variation and Taxonomic Considerations

When combining the analyses of similarities and differences in morphological characters with the cluster and canonical discriminant analyses between populations, a pattern of differences within and between nominal taxa appears. The major pattern persists, however, with the greatest differences between nominal taxa and with the *xanthina* species-group including the possibly more primitive *V. bulgardaghica* (Bulgar Daghi) as one subgroup, and the clearly monophyletic *raddei* species-group as a second subgroup. *Vipera bornmuelleri* (Bcharré and Mt. Hermon) is also well separated in all analyses from the *xanthina* populations, although showing much intraspecific variation. The geographically isolated single Urmia viper (*V. wagneri*) also differs in the cluster analysis from *xanthina* populations, although less spaced in the discriminant analysis. In morphological characters it is, however, clearly different from all available specimens of *xanthina* and *bornmuelleri*.

Vipera xanthina, on purely morphological grounds, can also be divided into two subgroups: a northern and northwestern assemblage of populations and a south Anatolian group of populations (Fig. 2—4, 31). This probably reflects an isolation since the Pleistocene with a following microevolutionary divergence.

The south Anatolian form of *xanthina* is characterized by a dark and well-developed rhombic zig-zag band along the back, and this consists of 26.1 ± 0.4 SE windings or blotches on the body, compared to 31.4 ± 0.6 SE in the northern form. Furthermore, it differs from the northern form by having a lower number of ventral plates (154 ± 0.6 SE, as compared to 162 ± 0.7 SE in northern *xanthina*). The southern *xanthina* has a comparatively light ground colour with only weakly developed white areas along the undulating dorsal band. In 56 % of the specimens, one or both of the two neck spots are united with the dorsal pattern, compared to 16 % in the northern *xanthina*. The dorsal ground colour is often much darker in the northern *xanthina*, often dotted with dark spots and blotches, while the areas between windings in the dorsal zig-zag band are much lighter in colour. This difference is more pronounced in females than in males.

Both groups have 23 midbody scale rows, but the northern group has on average a higher number of scale rows on the posterior part of the body. Half of the examined snakes have 17 and half 19 rows, while in the southern group all snakes have 17 rows. On the other hand, the southern group seems to have a higher count on the anterior part of the body. The mean value for the southern group is 23.7 ± 0.2 (range: 23—25), that for the northern group 22.9 ± 0.1 (range: 21—24).

The Sporadic group of *xanthina* differs from the north Anatolian subgroup in having a lower mean ventral value (158). This Aegean group, however, contains only four specimens and the ventral counts are all within the total range for the north Anatolian snakes. The mean value for the dorsal blotches is high (29.8) in the Aegean group, and agrees well with the mean number of blotches in the mainland north Anatolian populations (30.8). The Aegean specimens originate from the islands of Patmos (3) and Lipsos (1) in the Sporades close to the Turkish mainland. The Patmos specimens alone agree well with north Anatolian specimens in colour pattern and scalation, while the single Lipsos specimen, a female, differs from the mainland northern group as well as from the Patmos specimens in its rather low number of dorsal blotches (26) and, to some extent, ventral plates (157). The two females from Patmos had comparatively few ventrals (156 and 158) while the single Patmos male had 162. The mean value for the north Anatolian group is 162 ventrals, which is also the number found in a single female from the island of Kalymnos further south, as reported by Schneider (1983). In the two characters discussed above, the Lipsos female agrees with the south Anatolian populations. However, this individual differs from all specimens in both of the two mainland groups of populations, and in the Patmos population, in having a unicoloured belly without any traces of the characteristic half-moon shaped blotches on the ventral plates. Due to the scantiness of the material from this island, it is not possible at present to reach any further conclusion about the status of this single specimen. A

future study of additional material from Lipsos and perhaps of other Aegean islands would be highly desirable.

The coefficient of differences (CD) between the southern Anatolian population and the northern Anatolian population is 1.35 concerning the number of blotches and 1.25 regarding the number of ventral plates, including the single Lipsos specimen. According to Mayr (1969) the conventional level of subspecific differences is 1.28 when equal to 90 % of joint non-overlap. Our figures correspond roughly to 91 and 89 % of joint non-overlap in these characters respectively. The differences between the two groups in the characteristics discussed above are pronounced, and particularly striking is the absence of clines in the two groups. But in the light of the overall variation within *xanthina* as shown in the cluster and canonical analyses, we consider it most appropriate to treat the two groups taxonomically below the subspecies level.

As stated above, there are also some differences between the Mount Liban and the Mount Hermon populations of *V. bornmuelleri*. These two regions are separated by the Bekaa valley, which is a deep valley and probably a most effective geographical barrier, as *V. bornmuelleri* does not occur below 1 800 m altitude. The Mount Liban population has a pronounced sexual dimorphism in which many females tend to retain a juvenile pattern (Fig. 5 D) as adults, while the males normally have only a rudimentary pattern left, giving an *aspis*-like pattern. The lectotype of *bornmuelleri* (Werner 1922) is of this kind and, therefore, probably a male. Also, some Mount Liban males are very light in ground colour, resulting in a whitish or silvery appearance.

Based on the available material the Mount Hermon population seems to be sexually less dimorphic, and both males and females have a more irregularly barred pattern. The Mount Hermon specimens also seem to have a higher number of intercanthals and intersupraoculars. Obviously, there also seem to be differences in size between specimens from the two populations. The largest size of the 19 specimens examined from Mt. Liban (Bcharré region) was 53.8 cm. In the literature, the species is generally considered to be a dwarf species (Werner 1898; Müller & Wettstein 1933; Mertens 1967) — based on material from the same locality. The Mt. Hermon specimens grow much larger (maximum size 75.6 cm). Newborn specimens raised by us in captivity reached 40 cm within one year, and a two-year-old male measured 60 cm.

The intercanthals range between 9 and 16 (\bar{x} = 13.9) in Mt. Liban populations, and between 10 and 19 (\bar{x} = 15.7) on Mt. Hermon. Corresponding figures for the intersupraoculars are 30–41 (34.9) and 32–42 (35.8). The crown scales together are 42–54 (48.7) on Mt. Liban, and 42–61 (51.4) on Mt. Hermon. Lowest numbers of interocular rows separating supraoculars are 6–8 (7.1) on Mt. Liban, and 8–9 (8.3) on Mt. Hermon. The last figures correspond to slightly more than 80 % of joint non-overlap (CD = 0.96) in this character. These scalation differences appear to represent the beginning of an evolutionary trend toward a condition of more fragmented scalation in the Mt. Hermon population.

The number of midbody scale rows is also lower in Mt. Liban specimens when compared to the larger Mt. Hermon vipers. In the latter, there are always 23 scale rows, while

42 % of the Mt. Liban vipers have only 21 midbody scale rows. The mean value for the 19 Mt. Liban specimens is 22.1, which is close to 22.2, the figure mentioned by Mertens (1967) for *Vipera bornmuelleri*. Mertens' entire material came from the Mt. Liban population (Bcharré).

It may be argued that the scalation and size differences between the *bornmuelleri* populations represent a rather high differentiation, and the groups have certainly been separated since the Pleistocene and perhaps even longer. It is a question of opinion whether these populations merit taxonomic recognition; a study of genetic and etho-ecological differences, based on living specimens from both areas, may resolve this problem. However, at present we prefer to treat these two groups below the subspecies level.

Within the monophyletic *raddei* species-group, there seems to be less intra- and inter-specific variation than in the *xanthina* group, perhaps reflecting a younger origin with a less divergent speciation. There is, however, a clear pattern of four population systems comprising the Lar population (*latifii*), the Zanzan population (*albicornuta*), the Rezaeyeh-Khoy populations (southern *raddei*), and the Turkish and USSR populations (northern *raddei*). This is the overall picture emerging, when considering the different analyses and isolated morphological characteristics.

The two *raddei* forms are the only subgroups on a corresponding level in the entire *xanthina* complex that are separated by a great geographical distance. The unique inverted trunk pattern and colour that characterize the northern subgroup have only to some extent evolved (or are retained) in the southern populations. This, together with a combined analysis of all characters, as seen in the cluster and canonical discriminant analyses, shows that the two *raddei* groups have differentiated apart from each other. The large sandy and hilly areas that characterize the northern border region between Iran and Turkey and the regions north of Khoy in Iran have probably effectively separated these two *raddei* groups from each other during geologically younger periods. Accordingly we treat the southern Iranian form as a distinct taxon deserving subspecies designation.

SPECIES ACCOUNT

Vipera albicornuta Nilson & Andrén, 1985

Type locality: The holotype (RSI 3098) was collected at Abhar in the Zanjan valley, between Tabriz and Teheran, NW Iran. Leg. M. Latifi 1971.

Definition and diagnosis: A species of viper within the *Vipera raddei* species-group with raised and angled supraocular plates, which are separated from eye by circumocular scales, the latter completely surrounding the eye. The taxon is characterized by having a well developed and angled dark brown zig-zag band along the back. The dorsal band is finely black edged. Groundcolour is greyish brown. Neck pattern is consistently made up by two drop-shaped slightly oblique blotches, which are deep black in colour, sharply contrasting to other colours on the body. Similar deep dark bands run from posterior border of eye to corner of mouth and from lower border of eye down to mouth. A pronounced light dark-edged spot on each supraocular plate. Dark transverse spots along sides of body. Tail in males comparatively long (8.3–9.2 % of total length) with a high subcaudal count (35–38).

The species differs from its close relatives *Vipera raddei* and *V. latifii* in colour and pattern by having a well developed black-edged zig-zag band, very contrasting black markings on neck and sides of head, as well as very pale contrasting supraoculars. The black-edged dorsal pattern in *Vipera albicornuta* consists of about 44 to 52 windings, while in *V. raddei* the normally much reduced pattern consists of 34 to 45 more or less diffuse light blotches, meanwhile fused into a wavy dorsal band. The males of *albicornuta* have a longer tail (8.7–9.2 % of total length) than males of *V. raddei* (5.5–8.2 %), and a higher subcaudal count (35–38 compared to 29–34, $\bar{x} = 31.9$, in male *raddei*). Further the number of ventrals is lower in males of *albicornuta* (165–171) compared to male *raddei* (167–181, $\bar{x} = 174.3$), and the number of scales on crown of head (intercanthals + intersupraoculars) is less (34–40 compared to 40–52, $\bar{x} = 44.4$ in *raddei*).

From *Vipera latifii*, *V. albicornuta* differs in pattern, as *latifii* shows a marked polymorphism and a varying degree of reduced pattern. Further *V. albicornuta* has only two apicals in contact with rostral while three apicals in contact with rostral seems to be normal in *V. latifii*. Further the species has fewer first and second circumocular scales ($\bar{x} = 13.6$ and 14.5 respectively) than the *raddei* subspecies ($\bar{x} = 14.5$ – 14.7 for first and 15.2 – 15.3 for second circumocular rings). However the numbers are slightly higher than in *latifii* ($\bar{x} = 12.7$ and 14.1 respectively).

Description (morphology based on three preserved males and colour pattern on several photographed living specimens): Total length for the three preserved males (type-series) varies between 57.3 and 66.0 cm, while tail length varies between 8.7 and 9.2 % of total length.

Dorsal ground colour greyish brown, with a medium brown black-bordered zig-zag band along the back. The dorsal band consists of about 44 to 52 windings and is separated from the oblique droplike black spots on posterior part of head. Two small

central dark dots anterior to the dark drop-like spots. The pronounced light and contrasting spots on the supraoculars are very constant and distinct, particularly in living specimens. Laterally on the head a broad black band runs from posterior border of eye to corner of mouth, and a second similar band runs from eye down and slightly backwards to the border of the upper lip. A row of large dark blotches runs laterally on body, with each blotch covering about the first four scale rows on the area between the windings of the zig-zag band. Belly dark mottled with somewhat larger dark spots along the posterior edges of the ventrals. Throat and labials whitish with some black stippling.

Top of head covered by two large supraoculars, which are separated from the eye by circumocular scales. The outer edge of the supraocular is bent in right angle and protruding, giving an appearance of a small horn or markedly raised eyebrow. The supraoculars are separated from each other by seven interocular scales at shortest distance. The number of intersupraoculars is 24 to 28. Two canthal scales on each side separate supraoculars and supranasals. Two apicals bordering rostral. Number of intercanthals 12 to 16, and with a total number of scales on top of head (intercanthals + intersupraoculars) of 39 to 40. Eye separated from supralabials by two subocular scales (interoculolabials) in two specimens and by a single one in the third examined specimen. Eye surrounded by a complete first inner circumocular ring containing 13 to 15 scales, and by a second outer ring containing 13 to 17 scales. Nostril in the middle of a big nasal shield, which is partly fused with the prenasal. Upper preocular separated from the nasal by a loreal. Nine supralabials and eleven or twelve sublabials on each side. Two large anterior chinshields followed by four posterior chinshields. Two (or three) preentrals followed by 165 to 171 ventrals and 35 to 38 subcaudals (in males). A single anal shield. Dorsal side of body covered by 23 longitudinal scale rows one head length posterior to head, 22 and 23 on midbody, and 17 one head length anterior to anal.

Distribution (Fig. 32): According to Latifi (1984) *V. xanthina* ssp. (= *V. albicornuta*) is distributed in many areas in northern Iran. Specimens have been collected for the Razi Serum Institute from various parts of the Alburz mountains, the mountains surrounding the Zanjan valley, and from the northern parts of the Zagros mountains. The specimens here examined originate from Khan chai, Abhar and Zanjan (RSI) in the Zanjan valley, province Gilan, north Iran.

Habitat: Very sparse information is published on this taxon. Some general remarks on the mountains surrounding the Zanjan valley and on sympatric herpetofaunas are published with the description of the species (Nilson & Andrén 1985a). The Zanjan valley is surrounded by much sandy, but also partly rocky areas in a very dry region with sparse grass and bush vegetation, which also is heavily grazed.

Reproduction: No information is available.



Fig. 13: A group of *Vipera albicornuta*, at the Razi serum institute in Iran.

***Vipera bornmuelleri* Werner, 1898**

Vipera lebetina* var. *bornmuelleri Werner, 1902 (part.)

Coluber bornmuelleri Nikolsky, 1916 (part.)

Vipera lebetina xanthina Schwarz, 1936 (part.)

Vipera xanthina Werner, 1938 (part.)

Daboia raddei bornmuelleri Obst, 1983

Type locality: Type specimen collected by J. Bornmüller at 1800 m altitude in "Lebanon" 1897, and designated as lectotype by Werner (1922: 210, fig. 2a). Type specimen deposited in ZSM, but destroyed during World War II (Mertens 1967). *Terra typica restricta:* Bcharré, Mount Liban, Lebanon (Mertens 1967).

Definition and diagnosis: A species of viper within the *Vipera xanthina* species-group, characterized by having a much reduced dorsal pattern. This pattern is split up into small irregular bars and blotches, normally between 47 and 64 ($\bar{x} = 52$) on body. In young specimens the pattern is more similar to that in *V. xanthina*, while the central part of each dorsal blotch fades away during early growth, thus leaving only the dark edges of the blotches left. This results in an irregularly spotted or crossbanded pattern. Belly finely dotted without dark blotches. It is a species of small to medium size, often not exceeding 50 cm length in the wild, but can grow bigger.

Midbody scale rows 23 or more rarely 21. Comparatively short tail with only 23 to 26 subcaudals in females and 28 to 31 in males, compared to more than 27 in female *xanthina* and between 30 and 37 in male *xanthina*. Further it differs from *V. xanthina* and *V. wagneri* in having a lower ventral count (142 to 153, $\bar{x} = 147.8$ in females compared to between 148 and 169 in female *xanthina* and around 161 in female *wagneri*; and 144 to 152, $\bar{x} = 148.4$, in males compared to between 151 and 167 in male *xanthina*). *Vipera bornmuelleri* often has three apicals (62 %) in contact with rostral while *V. xanthina* and *V. wagneri* has two. Supralabials nine on each side, while *V. xanthina* regularly has ten.

Vipera bornmuelleri differs from *V. bulgardaghica* by not having the upper preocular in contact with nasal, in having 21 or more scales in first circumocular rings (counted together), and 25 or more in second rings (21 or less in first and 25 or less in second circumocular rings in *V. bulgardaghica*), and in having 2 scale rows between eye and supralabials (one in *V. bulgardaghica*). *Vipera bornmuelleri* is also separated from *xanthina* and *bulgardaghica* by having a higher number of intercanthals and intersupraoculars (42–60 counted together, compared to between 30 and 50 in the latter two).

Description (based on 17 females and 13 males): Maximum size for western Mt. Liban females is 47.3 cm and for males 53.8 cm. Eastern Mt. Hermon specimens grow bigger. One male (NMB 21020) from Mt. Hermon measured 56.5 cm while two females from the same locality measured 60.0 cm (NMB 21014) and 75.6 cm (ZIG). Tail measures between 7.0 and 10.0 % of total length in females and between 8.7 and 10.0 % in males.

Ground colour greyish to brownish with a darker dorsal pattern. Males tend to be lighter in ground colour. Dorsal pattern dark brownish occasionally surrounded by whitish areas and consisting of 47 to 64 ($\bar{x} = 52$) irregular transverse bars or blotches. Neck pattern consisting of two oblique spots only rarely united with first dorsal spot (14 %). Belly pattern unicoloured greyish, often with fine punctation. A dark band from posterior border of eye to the corner of mouth. A series of smaller dark spots laterally on each side of body.

Crown of head covered by two large somewhat convex supraoculars which are in broad contact with eye and separated from each other by a row of 6 to 9 ($\bar{x} = 7.4$) interocular scales at shortest distance. Total number of intersupraoculars 31—42 ($\bar{x} = 35.3$). One to one and a half ($\bar{x} = 1.3$) canthal scales on each side separating supraoculars and supranasals. Two or three ($\bar{x} = 2.6$) apicals bordering rostral. Total number of intercanthals 9—19 ($\bar{x} = 14.6$) and with a total number of scales on top of head (intercanthals + intersupraoculars) ranging from 42 to 61 ($\bar{x} = 50.1$). Eye separated from supralabials by two subocular rows (in one case three) and surrounded by a first inner and a second outer circumocular ring containing 11—15 ($\bar{x} = 12.3$) and 13—16 ($\bar{x} = 14.8$) scales respectively. Nostril in the middle of a big nasal shield, which is partly fused with the prenasal. Upper preocular somewhat rectangular and rarely penetrating somewhat in between canthal and loreal towards nasal. However, always separated from nasal by at least the distance of half the loreal. Nine supralabials on each side in 68 % of the specimens while 28.5 % have ten on one side of head. No specimen had



Fig. 14: A male *Vipera bornmuelleri* from Mt. Hermon (Israel administered area) (ZIG).

ten on both sides. 3.5 % had 8 supralabials on one side and 9 on the other. Eleven to thirteen ($\bar{x} = 12.0$) sublabials on each side. Two large anterior chinshields followed by four to six ($\bar{x} = 4.8$) posterior chinshields. One to three ($\bar{x} = 1.9$) prementals followed by 142 to 153 ($\bar{x} = 147.8$) ventrals in females and 144 to 152 ($\bar{x} = 148.4$) ventrals in males. A single anal shield. Subcaudals 23 to 26 ($\bar{x} = 25.6$) in females and 28 to 31 ($\bar{x} = 29.5$) in males, in double rows except the last spine. Dorsal side of body covered by 23 to 25 ($\bar{x} = 23.3$) longitudinal scale rows one head length posterior of head, 21 to 23 ($\bar{x} = 22.5$) on midbody, and 15 to 19 ($\bar{x} = 16.8$) one head length anterior to anal.

Distribution (Fig. 32): *Vipera bornmuelleri* is represented in museum collections and literature from five different localities: Bcharré (ZSM; NMW; SMF; Schwarz 1936; Müller & Wettstein 1933; Mertens 1967) and Les Cedres (Cedars of Lebanon) (BM; MHNG), which are rather close to each other and situated on the western slopes of Mount Liban (High Lebanon); at Faraya, which is further south in the same mountain range (Zinner 1967; HUIR), Chouf, northeast of Saida (Hraoui Bloquet 1981), and on Mount Hermon (Jebel esh Sheikh, Mitzpe Shalkim-Hermon) on the Lebanon-Syria border (NMB; SMF; ZIG; HUIR; TAU; Mendelssohn in litt.; Werner & Avital 1980; Esterbauer 1985). Total range for the species is not known but, besides Mount Liban and Mt. Hermon on each side of the Bekaa valley, the high mountains of Anti-Lebanon (Jebel ash Sharqi) further north on the Lebanon-Syria border could also be expected to be a part of the range. The discovery of *V. bornmuelleri* on Mt. Hermon increased the known range into Syria and Israel-administrated territory.

Habitat: Comparatively little information is available on habitat choice but some data are published. Werner & Avital (1980) stated that the species is restricted to an altitudinal zonation of between 1800 and 2000 m on Mt. Hermon. These figures agree well with information on museum specimens from Cedres on Mount Liban (BM specimens), and from Faraya where Zinner (1967) collected it at 1900 m altitude. Also specimens collected at Bcharré are from 2000 m altitude (Müller & Wettstein 1933). Hurvitz (1980) gives 1500 to 2814 m as the altitudinal range on Mt. Hermon which is also verified by Esterbauer (1985), and Mendelssohn (in litt.) says that the species occurs down to 1600 m. This is also the altitude (5300 feet) for the HUIR specimen collected 3 km NE of Faraya in Mount Liban. Hraoui Bloquet (1981) recorded it at Chouf in the same mountain range, which is situated at about 1450 m altitude.

The western slopes of Mount Liban, at Bcharré and Les Cedres, are partly covered with rich vegetation because of the heavy precipitation in the region (Zinner 1967). According to the same author, the rich vegetation ends at 2000 m altitude. The area above 2000 m was in past times covered by huge cedar forests both at Bcharré and at Faraya.

Reproduction: Several matings followed by birth have been observed at the Tel-Aviv University with captive Mt. Hermon specimens (Mendelssohn in litt.). Birth has taken place in captivity as late as early September, and one female gave birth to a clutch of 6 and another to a clutch of 18 young. Groombridge (1986) cites information on clutch sizes of two and five young, also born at Tel-Aviv University.

Vipera bulgardaghica Nilson & Andrén, 1985

Vipera bornmuelleri Werner, 1898 (part.)

Vipera lebetina var. *bornmuelleri* Werner, 1902 (part.)

Vipera lebetina xanthina Schwarz, 1936 (part.)

Vipera xanthina Mertens, 1967 (part.)

Vipera c.f. *xanthina* Joger, 1984 (part.)

Type locality: Type specimens collected by Martin Holtz 1897 at "Kar Boghaz", Bulgar Dag, Cilician Taurus in south central Anatolia, at 2500 m altitude. Holotype (GNM 1618) deposited in Göteborg Natural History Museum, Sweden.

Definition and diagnosis: A subalpine species of *Vipera* within the *xanthina* species-group and characterized by having subocular scales in contact with supralabials; upper preocular close to or in contact with nasal; a reduced number of first and second circumocular scales; a pattern consisting of around 40 rhombic or right-angled zig-zag windings along the back, and a more or less pronounced transverse "bridle" across the snout.

Midbody scale rows 23 in number. Nine supralabials and often three apicals in contact with rostral (ten supralabials and two apicals in *xanthina*). Tail relatively short with 29–33 subcaudals in males, compared to between 30 and 37 in male *xanthina*, and 26 in the single known female, compared to between 27 and 36 in female *xanthina*. Further it differs from male *xanthina* in having a lower ventral count (150–154, compared to between 151 and 167 in male *xanthina*), and from female *xanthina* and *wagneri* in having only 145 ventrals compared to between 148 and 169 in female *xanthina*, and 161 in the single known female *wagneri*. Further it differs from *xanthina* in having belly finely dotted or with weakly developed dark spots (larger dark spots in *xanthina*).

Vipera bulgardaghica differs further from *V. bornmuelleri* by having a lower number of intercanthals and intersupraoculars (35–43 compared to between 42 and 58 in *bornmuelleri*).

The number of windings in the dorsal zig-zag band is between 40 and 46 in *bulgardaghica* compared to between 47 and 64 in *bornmuelleri*, and between 22 and 41 in *xanthina*.

Description (based on one female and two males): The female measures 52.0 cm total length and the larger male 59.1 cm. Tail measures 4.3 cm (= 8.2 % of total length) in the female, and between 8.1 and 9 % of total length in males.

Ground colour brownish grey. No marked sexual colour dimorphism. Sinuous dorsal band pronouncedly right-angled, or partly consisting of more or less round or squarish dark blotches. Blotches with more whitish interspaces in the female. The colour of the dark blotches and sinuous band is somewhat reduced in intensity in central parts. The neck pattern consists of two oblique, isolated blotches. Belly pattern finely dotted with only very weakly developed dark spots.

Top of head covered by two large supraoculars, which are in broad contact with eye and separated from each other by a row of six interocular scales at their shortest distance. Total number of intersupraoculars is 24–36 (\bar{x} = 30.0). One canthal scale

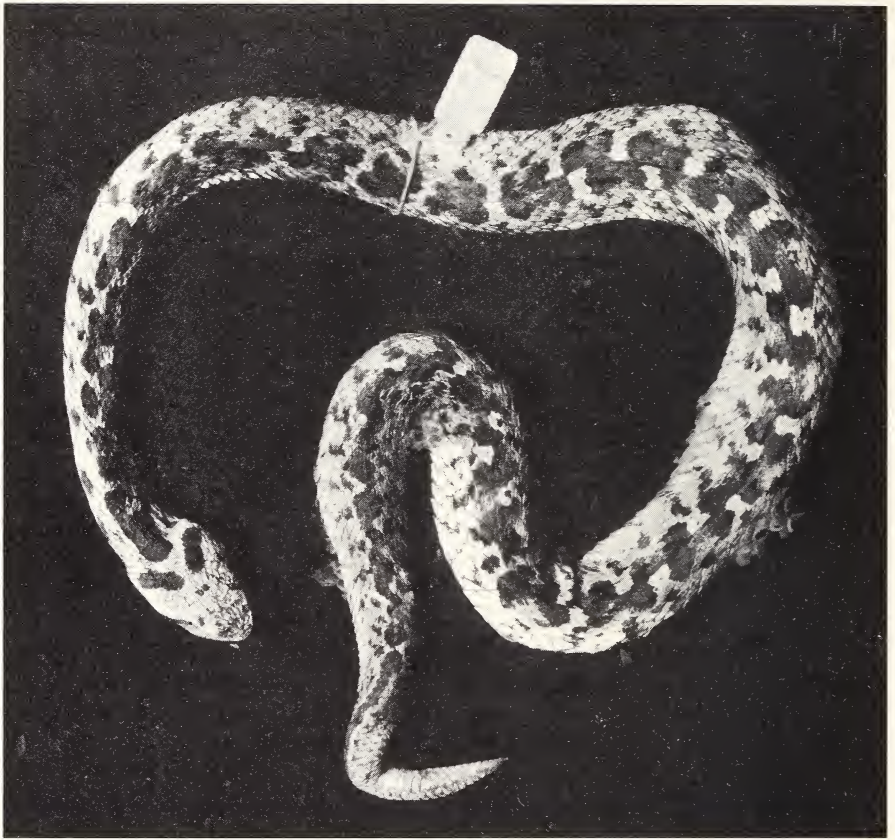


Fig. 15: Holotype of *Vipera bulgardaghica* (GNM-Re. ex.1618) from Bulgar Dag (Bolkar Dagi), South Central Turkey.

on each side separating supraoculars and supranasals. Two or three ($\bar{x} = 2.6$) apicals bordering rostral. Total number of intercanthals 8–13 ($\bar{x} = 10.7$) and with a total number of scales on top of head (intercanthals + intersupraoculars) ranging from 35 to 43 ($\bar{x} = 40.3$). Eye separated from supralabials by a single subocular (interoculolabial), at least on one side of head, and surrounded by a first inner and a second outer circumocular ring, containing 9–11 ($\bar{x} = 10.0$) and 10–13 ($\bar{x} = 11.3$) scales respectively. Nostril in the middle of a big nasal shield, which is partly fused with the prenasal. Upper preocular somewhat rectangular and reaching nasal or nearly so. Nine supralabials on each side. Eleven to thirteen ($\bar{x} = 11.5$) sublabials on each side. Two large anterior chinshields followed by four posterior chinshields. Two preventrals followed by 145 ventrals and 24/26 + 1 subcaudals in the female, 150–154 ventrals and 32/33 + 1 and 28/29 + 1 subcaudals in the two males respectively.

A single anal shield. Dorsal side covered by 23 to 25 ($\bar{x} = 24.3$) longitudinal scale rows one head length posterior of head, 23 to 25 ($\bar{x} = 23.7$) on midbody, and 17 one head length anterior to anal.

Distribution (Fig. 32): *Vipera bulgardaghica* is so far only recorded on the type locality: Kar Boghaz, Bulgar Dag (Bolkar Dag) at 2500 m in Cilician Taurus, Prov. Nigde, south central Anatolia (Werner 1898; Nilson & Andrén 1985 b).

Habitat: The area where the species was collected is situated in the subalpine region, which extends between 2100 and 2700 m altitude in the Bulgar Dag mountains. This zone is characterized by open thorn-cushion formations, grasslands and perennial forb communities and topographically by high mountain rock and scree formations, surrounded by large gravel fields and hills. The mountains consist of crystalline limestone and marble which are heavily eroded and the few remaining rock areas are isolated from each other by large areas of decomposed and weathered materials. Permanent snowfields occur in the region.

Reproduction: Nothing is known.

***Vipera latifii* Mertens, Darevsky & Klemmer, 1967**

Daboia raddei latifii Obst, 1983

Type locality: Upper Lar Valley, southwest of Mt. Demarvand in the Alburz mountain chain of northern Iran, northeast of Teheran. Altitude of 2180–2900 m. Holotype (SMF 62585) collected by Dr. M. Latifi 1.—2. 10. 1966 and deposited in Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt a.M. Nine of the 14 paratypes, which all have the same data as holotype, are deposited together with the holotype in Frankfurt (SMF 62586–94), while three (ZIN 17977 a–c) are in Zoological Institute, Academy of Sciences, Leningrad and two (MHNG 1324.44–45) in Muséum d' Histoire Naturelle, Genève (collection Kramer). Topotypical specimens bearing the same date and collector are deposited in Teheran (RSI) and Göteborg (ZIG).

Definition and diagnosis: A species of the *raddei* species-group characterized by a great polymorphism in dorsal pattern and many scalation characters. Pattern can consist of a dark dorsal zig-zag band, dark diffuse blotches, a narrow vertebral line, or can be totally missing. Belly finely dotted. Dorsal ground colour varies between brownish, brownish grey, greyish or yellowish grey. Supraocular plate angled and raised, separated from eye by circumocular scales which form a complete circumocular ring. Maximum size 78 cm.

Closely related to *Vipera albicornuta* and *V. raddei* but differs from the first by having a much reduced pattern and a pronounced polymorphism. *V. albicornuta* has a pronounced dorsal zig-zag band, which is markedly black-edged and which shows little variation. Further *V. latifii* normally has three apicals in contact with rostral while *V. albicornuta* has two.

Differs from *V. raddei* in the number of ventrals, which are ranging from 162 to 169 ($\bar{x} = 165$) in male *V. latifii* and between 161 and 166 ($\bar{x} = 164$) in females (between

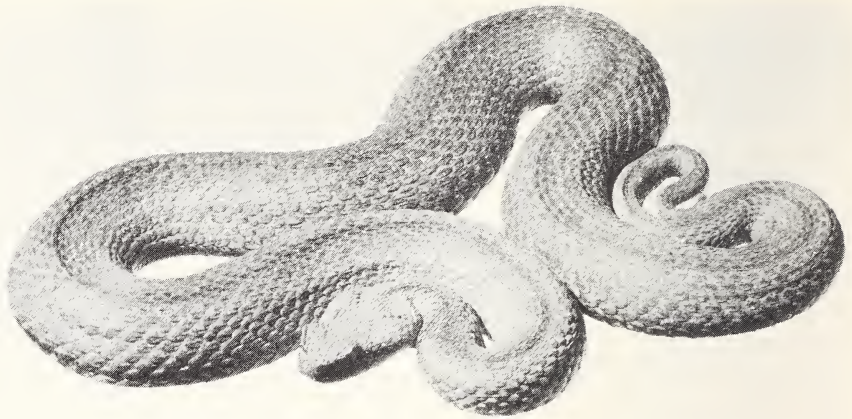


Fig. 16: A male *Vipera latifii* from the Lar valley, with weakly developed vertebral line (ZIG).

167 and 178, $\bar{x} = 173.8$, in male *raddei* and between 165 and 179, $\bar{x} = 170.6$, in female *raddei*). The number of subcaudals ranges between 29 and 39 ($\bar{x} = 34.3$) in males and between 27 and 34 ($\bar{x} = 29.7$) in females. Corresponding counts in *raddei* are 29—34 ($\bar{x} = 32.2$) in males and 28—32 ($\bar{x} = 29.8$) in females.

Relative tail length varies in adult males between 7.0 and 11.1 % ($\bar{x} = 8.8$ %) of total length, and in adult females between 6.2 and 9.4 % ($\bar{x} = 7.8$ %). Corresponding measurements in *V. raddei* are 5.5—8.2 ($\bar{x} = 7.0$ %) of total length in males and 5.4—7.7 ($\bar{x} = 6.9$ %) in females. Number of prefrontals ($\bar{x} = 2.1$) is less than in *raddei* ($\bar{x} = 2.9$ —3.0). Number of scales in first circumocular ring ($\bar{x} = 12.7$) is less than in the subspecies of *raddei* ($\bar{x} = 14.5$ —14.7), and slightly less than in *albicornuta* ($\bar{x} = 13.6$). Number of scales in the second circumocular ring ($\bar{x} = 14.1$) is also less than in *raddei* ($\bar{x} = 15.2$ —15.3), and to some degree less than in *albicornuta* ($\bar{x} = 14.5$).

Description (based on 19 females and 17 males): Maximum size for females is 70.0 cm and for males 78.0 cm. Tail measures between 6.2 % and 9.4 % of total length in females and between 7.0 % and 11.1 % in males.

Colour varies between brownish, greyish, brownish grey or yellowish grey, with a very variable pattern that also can be totally missing. No sexual dimorphism in colour pattern. The dorsal pattern can consist of a rather well developed narrow vertebral line, one to two scales wide, and which can be connected with a varying number of alternating or opposite blotches. Those blotches can be just a few, or more regularly between 36 and 54, forming a more typical zig-zag band. Occasionally the central vertebral line is missing leaving only the alternating blotches left, which results in a spotted or blotchy pattern. Normally this last type of pattern is less contrasting or pronounced than the developed zig-zag band. Some specimens have a series of alternating darker spots laterally on body. The ground colour can also be finely dotted with dark, occasionally only laterally on flanks. Neck pattern consists of two more or less developed oblique spots, which may be missing in unicoloured specimens. Belly finely dotted.

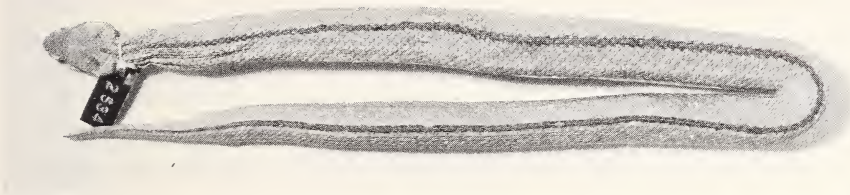


Fig. 17: A female *Vipera latifii* from the Lar valley, with sharply developed vertebral line (RSI 2534).

Crown of head covered with two large supraoculars, which are separated from eye by circumocular scales. The outer edge of the supraoculars is protruding in right angle, giving an appearance of a small horn or markedly raised eyebrow. The supraoculars are separated from each other by seven to nine ($\bar{x} = 7.4$) interocular scales at shortest distance. Total number of intersupraocular scales is 21 to 35 ($\bar{x} = 26.9$). The number of canthals on each side separating supraoculars from supranasals varies between 1.75 and 3.5 ($\bar{x} = 2.15$). Two, or more often three ($\bar{x} = 2.6$) apicals bordering rostral. The number of intercanthals is 10 to 20 ($\bar{x} = 14.7$) and with a total number of scales on top of head (intercanthals + intersupraoculars) of between 35 and 48 ($\bar{x} = 41.6$). Eye separated from supralabials by two suboculars (one row on both sides of head in two specimens, one row on one side of head and two on the other in three specimens). Eye surrounded by a complete first inner circumocular ring containing 10 to 15 ($\bar{x} = 12.9$) scales, and by an outer ring containing 12 to 16 ($\bar{x} = 14.1$) scales. Nostril in the middle of a big nasal shield, which is partly fused with the prenasal. Upper preocular separated from the nasal by a loreal. Eight to twelve ($\bar{x} = 9.3$) supralabials and nine to thirteen ($\bar{x} = 11.9$) sublabials on each side. Two large anterior chinshields followed by four to seven ($\bar{x} = 4.5$) posterior chinshields.

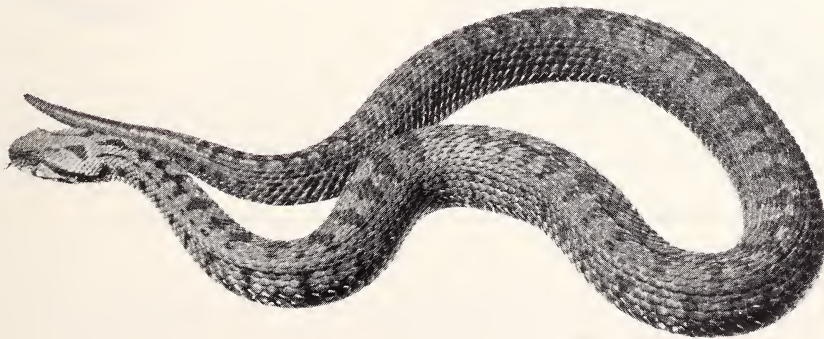


Fig. 18: A male *Vipera latifii* from the Lar valley, with dorsal zig-zag band (ZIG).

One to three ($\bar{x} = 2.1$) prefrontals, followed by 161 to 166 ($\bar{x} = 163.6$) ventrals in females, 162 to 169 ($\bar{x} = 165.1$) ventrals in males, and 26 to 34 ($\bar{x} = 29.7$) subcaudals in females, 29 to 39 ($\bar{x} = 34.3$) subcaudals in males. A single anal shield. Dorsal side of body covered by 17 to 25 ($\bar{x} = 22.7$) longitudinal scale rows one head length posterior to head, 21 to 23 ($\bar{x} = 22.8$) on midbody, and 16 to 18 ($\bar{x} = 17.0$) one head length anterior to anal.

Distribution: Restricted to the Alburz mountains range. Originally known only from the upper Lar valley, about 60 km northeast of Teheran, at an altitude of between 2180 and 2900 m (Andrén & Nilson 1979). Localities given by the Wildlife Protection Society in Iran (F. Sayadoghly in litt., 1984, to Brian Groombridge, IUCN) includes Teheran, Lar valley, Damavand, Firozkoh and Aba-ask, but several of these observations are probably hinting at *V. albicornuta* (*V. xanthina* ssp., sensu Latifi 1984), which also occurs in parts of the Alburz mountains. According to Groombridge (in litt.) it is not clear whether there are actual records of *V. latifii* from the places outside the Lar valley.



Fig. 19: A female *Vipera latifii* from the Lar valley, with blotchy pattern (ZIG).

The Lar valley, about 70 km long with a mean width of 7 km, has several smaller side valleys. Since the late 1970 a major part of the valley has been submerged due to the construction of a huge water reservoir in the valley and it has not been possible to establish which range is left for the species.

H a b i t a t : The habitat consists of rocky areas with large boulders along the steep, well-drained and sparsely vegetated hillsides of the upper Lar valley. The region is characterized as high, alpine steppe (Zohary 1973) and includes typical steppe habitats, rocky habitats and alpine zones with permanent glaciers. *Vipera latifii* inhabits the narrow zone between the steep mountain walls and the flat lower plains of the valley, a sparsely vegetated zone characterized by moulds of weathered rocks and boulders. The vegetation in the area where the steppe habitat meets the rocky zone, and where *V. latifii* occurs, includes *Ferula*, *Stipa*, *Astragalus*, *Verbascum*, *Eremurus spectabilis*, *Onobrychis cornuta*, *Euphorbia*, *Salvia*, *Tulipa* and *Iris* (see Andrén & Nilson 1979 for further description of the habitat).

R e p r o d u c t i o n : During a field study in the Lar valley in 1976, courtship display was observed in mid-June, which is later in the season than in congeneric species. Three females collected during the same period were all pregnant and later gave birth to three clutches at the Department of Zoology in Göteborg (Andrén & Nilson 1979) on the 26th to 29th of September, three and a half months later. Additional matings occurred in captivity during 1981, 1982, 1983 and 1985. In 1981 a male and female, both with well-developed zig-zag bands, mated on the 10th of April and a clutch of nine young, all with well-developed zig-zag band, was born on the 19th of July, after slightly less than three and a half months. In 1982 a male and a female, both with dorsal pattern of diffuse blotches, mated on the 7th of April and the female gave birth to ten young on the 13th of July, after slightly more than three months. All young in this clutch had dorsal patterns of diffuse blotches. In 1983, a male with diffuse blotchy pattern mated with a female with zig-zag band on the 18th of March, which resulted in a clutch of ten young, all with blotchy patterns, on the 5th of July. Again the pregnancy period lasted for about three and a half months. Most of the young in these clutches have been raised to adult stage and the dorsal pattern has not changed with growth.

Of the three originally wild caught pregnant females one, which had a well developed dorsal zig-zag band, gave birth to nine young, all with dorsal zig-zag bands. One female with diffuse blotches and one with zig-zag band gave birth to six young with blotchy pattern, two young with zig-zag pattern, and two with dorsal pattern of a narrow vertebral line, during the same night in the same terrarium; in this last case, juvenile pattern can not be related to female pattern type. Both of these last females were of the same size and produced half of the young each.

The mean clutch size of the first six clutches is 8 ± 0.96 SE with a range of between 5 and 10 juveniles. The mean weight in the different clutches varies between 4.15 and 5.97 g, while the mean length in the clutches varies between 15.9 and 19.4 cm. The overall mean for all juveniles together (48) is $5.01 \text{ g} \pm 0.10$ SE and $17.7 \text{ cm} \pm 0.43$ SE for weight and length respectively. Minimum and maximum values in weight are 3.39 and 6.52 g, and in length 15.5 and 20.0 cm. In 1985 three more clutches were produced with 2, 9, and 13 juveniles.

Vipera raddei raddei Boettger, 1890

Vipera raddii Boulenger, 1896

Coluber raddei Nikolski, 1916

Vipera lebetina raddei Schwarz, 1936

Vipera xanthina raddei Mertens, 1952

Daboia raddei raddei Obst, 1983

Type locality: Original description based on two specimens from Kasikoparan/Armenia (40°02'N, 43°26'E) (Boettger 1890), a place nowadays situated in Turkey (Kazikkiran (= Kazikkoparan), Tuzluca, province Kars, N.E. Anatolia) (Baran 1976). The types were collected in 1880 by Christoph and sent to Boettger from G. V. Radde. Specimens of *Vipera raddei* were earlier depicted by Strauch (1869) under the name *V. xanthina* (Gray), and in a later work Strauch (1874) mentioned a specimen collected by Radde at Nachitschewan Tschai. Boettger includes this last locality as part of the range for the species in his description of *V. raddei*. The designation of Nachitschewan Tschai as terra typica restricta (Schwarz 1936), must however be rejected according to Art. 72e in The Roles of Zoological Nomenclature. The two type specimens were deposited in the Georgian Museum in Tbilisi, but have later perished (Darevsky in litt.). A topotypic specimen (BM 6.7.96) collected by G. V. Radde is in the British Museum (Natural History).

Definition and diagnosis: A northern subspecies of *raddei* characterized by a reversed or inverted colour pattern, consisting of a darker ground colour with a light dorsal band or markings. Ground colour greyish brown, brownish grey, greyish black or blackish. A dorsal band of often isolated, sometimes dark-edged and roundish blotches yellow, yellowish-orange, brown-orange or reddish in colour, and smaller than corresponding markings in *xanthina* or *albicornuta*. Transverse black-grey spots on sides of body, often diffuse. Belly blackish in colour. Neck pattern consists of oblique, transverse or L-shaped black spots that may be united with the dorsal pattern on body. Supraocular plate angled and raised, separated from eye by circumocular scales. The latter form a complete circumocular ring. Maximum size around 100 cm.

Differs from the other two species in the *raddei* species-group (*albicornuta* and *latifii*) by having a relatively short tail (see Table 1), a higher number of ventrals (\bar{x} = 170.7 in females compared to 163.6 in female *latifii*; 174.3 in males compared to 165.0 in male *latifii* and 168.0 in male *albicornuta*), and a lower number of subcaudals in males (Table 1). The mean number of preentrals is 3.0 in *raddei*, compared to 2.1 in *latifii* and 2.3 in *albicornuta*; mean number of scales in first circumocular ring is 14.5 compared to 12.7 in *latifii* and 13.6 in *albicornuta*, and in second circumocular ring 15.2, compared to 14.1 and 14.5 in *latifii* and *albicornuta* respectively.

Description (based on 31 females and 42 males): Maximum size for females is 79.0 cm, and for males 99.2 cm. Tail measures between 5.4 % and 7.7 % of total length in females, and between 5.5 % and 8.2 % in males.

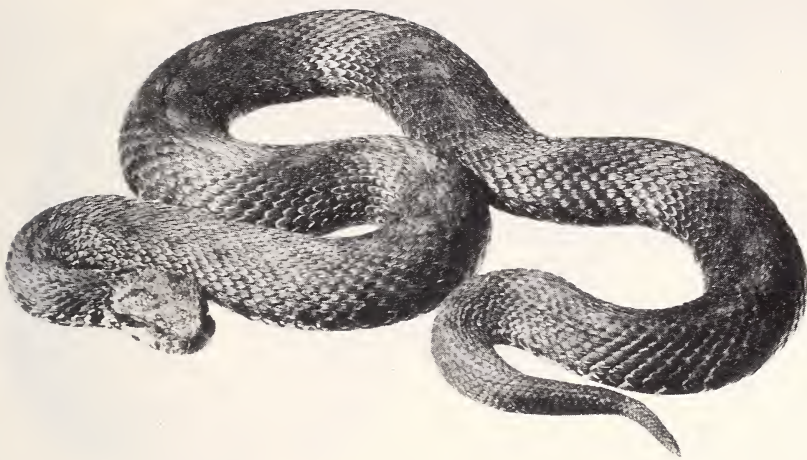


Fig. 20: A female *Vipera raddei raddei* from Digor, N.E. Turkey (ZIG).

Colour as in diagnosis. No pronounced sexual dimorphism in colour and pattern, but females tend to have slightly lighter snout. The dorsal pattern can sometimes be united to a narrower or broader zig-zag band, but consists most frequently of separated light, often round blotches that sometimes, and especially on lateral sides, are dark-edged with dark brown or blackish. The number of blotches is ranging from 34 to 46 ($\bar{x} = 41.6$). A series of alternating dark spots on lateral side of body. Neck pattern as in diagnosis. Belly blackish.

On top of head two large supraoculars, which are separated from eye by circumocular scales. The outer edge of the supraoculars is protruding in right angle, giving an appearance of a small horn or markedly raised eyebrows. The supraoculars are separated from each other by 6 to 9 ($\bar{x} = 7.4$) interocular scales at shortest distance. Total number of intersupraocular scales is 22 to 35 ($\bar{x} = 29.3$). The number of canthals on each side separating supraocular from supranasal varies between 1.75 and 3.0 ($\bar{x} = 2.1$). Two to five ($\bar{x} = 2.4$) apicals bordering rostral. The number of intercanthals is 11 to 24 ($\bar{x} = 14.9$), and with a total number of scales on top of head (intercanthals + intersupraoculars) of between 36 and 52 ($\bar{x} = 44.2$). Eye separated from supralabials by two subocular rows and surrounded by a complete first inner circumocular ring, containing 12 to 18 ($\bar{x} = 14.5$) scales and by an outer ring, containing 13 to 18 ($\bar{x} = 15.2$) scales. Nostril in the middle of a big nasal shield, which is partly fused with the prenasal. Upper preocular separated from the nasal by a loreal. Nine, or more rarely ten ($\bar{x} = 9.1$) supralabials, and ten to fourteen ($\bar{x} = 11.9$) sublabials on each side. Two large anterior chinshields, followed by 4 to 6 ($\bar{x} = 4.2$) posterior chinshields. 2 to

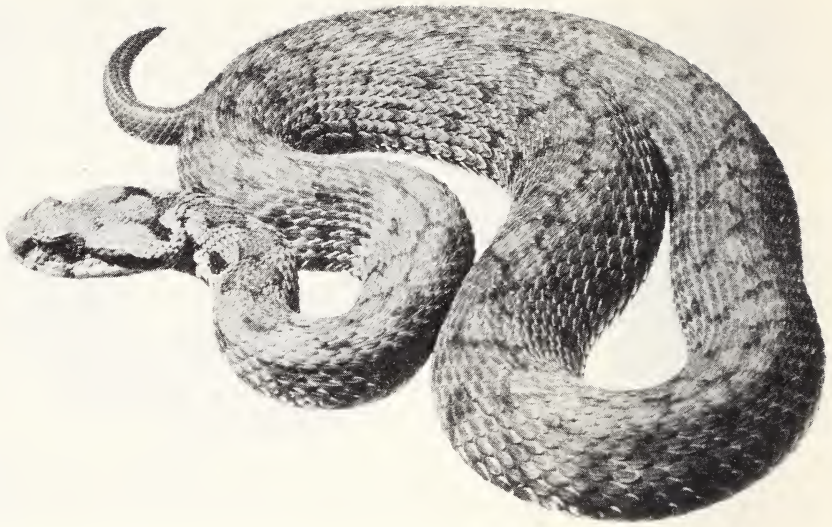


Fig. 21: A male *Vipera raddei raddei* from Mt. Ararat, N. E. Turkey (ZIG).

4 ($\bar{x} = 3.0$) prefrontals, followed by 163 to 179 ($\bar{x} = 170.7$) ventrals in females, 167 to 181 ($\bar{x} = 174.3$) ventrals in males, and 28 to 32 ($\bar{x} = 30.0$) subcaudals in females, 29 to 35 ($\bar{x} = 31.9$) subcaudals in males. A single anal shield. Dorsal side of body covered by 21 to 25 ($\bar{x} = 23.4$) longitudinal scale rows one head length posterior to head, 21 to 25 ($\bar{x} = 23.0$) on midbody, and 17 to 19 ($\bar{x} = 17.5$) one head length anterior to anal.

Distribution (Fig. 25): Known range includes easternmost Turkey, extreme northwestern Iran and adjacent USSR, which all are parts of the Armenian region. In USSR this taxon is restricted to parts of Nakhichevan ASSR and Armeniya SSR (see Fig. 25, based on Bannikov et al. 1977 for the USSR parts). From Turkey it is known from the type locality (Kazikkoparan Tuzluca, Kars), as well as from Mt. Ararat (Agri Dag), Subatan Kars, Ordubad (Aras river), Digor and Kagizman (Basoglu in litt.; Baran 1976; Schwarz 1936; Mertens 1952; ZIG, BM, MHNG, NMB). In Iran this taxon occurs in northwest Azarbaijan (BM).

Habitat: Habitat given by Darevsky (1966) for Armenian USSR as rocky, occasionally in steep and scraggy slopes, overgrown with thin oak forests. The species is most abundant among dry rocks, thin oaks and bushes and among rock fragments at wooded slopes. It also occurs in stony slopes with sparse growth of xerophytic oak and junipers as well as on xerophytic steppe. Sometimes also in cultivated land. The species is found in altitudes between 1.100 and 2.400 m (Groombridge 1986). In eastern Turkey it often seems to occur in ridges composed of volcanic lava blocks (Flärldh 1983; Sochurek 1984).

Reproduction: According to Darevsky (1966) mating takes place during May or even later in Armenian USSR. Birth takes place in early September, but can be delayed towards the end of that month. The pregnancy period seems to be around three and a half months in nature. Clutch size is 3 to 9.

Pregnancy varied between slightly more than three months to three and a half months in specimens from Digor, Turkey, which have been bred by us at the Department of Zoology, Göteborg.

The mean clutch size of five clutches is 5.8 ± 0.7 SE with a range of between 4 and 8 juveniles. Their mean weight in the different clutches varies between 7.6 and 11.08 g, while the mean length in the clutches varies between 20.0 and 21.57 cm. The overall mean for all juveniles together (29) is $9.28 \text{ g} \pm 0.3$ SE and $20.9 \text{ cm} \pm 0.18$ SE for weight and length respectively. Minimum and maximum values in weight are 5.76 and 12.61 g, and in length 19.5 and 23.4 cm.

Vipera raddei kurdistanica ssp.n.

Holotype: RSI 3128, an adult female from Rezaeyeh, west Azarbaijan, Iran. Leg. Dr. Mahmoud Latifi 1975. Fig. 22 a—b.

Paratypes: RSI 3117, 3118, same data as holotype; RSI 2778, 2789, 2834 and 2859 from Gotar and Razi, west Azarbaijan 1976—1978; RSI 2841 and 2842 from Khoy, west Azarbaijan 1977. Leg. Dr. M. Latifi.

Diagnosis: A very polymorphic southern subspecies of *V. raddei*, characterized by having all intermediate trunk pattern types. Pattern ranging from typical *raddei* pattern, with a series of light blotches or zig-zag windings on a dark ground colour (inverted or reversed pattern), through almost unicoloured, with a pattern very similar in colour to ground colour, towards a series of darker blotches on a very light ground colour (Fig. 6 b—c; Fig. 23—24). Ground colour variable, from light whitish grey through different shades of grey (grey, greyish beige, brownish grey, blackish grey). Belly pattern variable, from finely dotted on light ground to very dark with light spots. Head and neck pattern often reduced or absent. Supraocular plate angled and raised, separated from the eye by circumocular scales, which form a complete circumocular ring.

Differs from the two species in the *raddei* species-group (*latifii* and *albicornuta*) by having a relatively short tail (less than 7.5 % of total length in both sexes; more in *latifii* and *albicornuta*); 172 or more ventrals in males (less in males of the compared species) and 165 or more ventrals in females (166 or less in female *latifii*). Further this taxon has a slightly higher number of first circumoculars ($\bar{x} = 14.7$, compared to 12.7 in *latifii* and 13.6 in *albicornuta*) and second circumoculars ($\bar{x} = 15.3$, compared to 14.1 in *latifii* and 14.5 in *albicornuta*). Normally around three ($\bar{x} = 2.9$) prefrontals compared to around two in *latifii* ($\bar{x} = 2.1$) and *albicornuta* ($\bar{x} = 2.3$). Male *kurdistanica* are also separated from male *albicornuta* by having fewer subcaudals (32—33, compared to 35 or more in *albicornuta*).



Fig. 22: Holotype (RSI 3128) of *Vipera raddei kurdistanica* ssp. n. Female from Rezaeyeh, west Azarbaijan, Iran. a) Dorsal side and b) Ventral side.

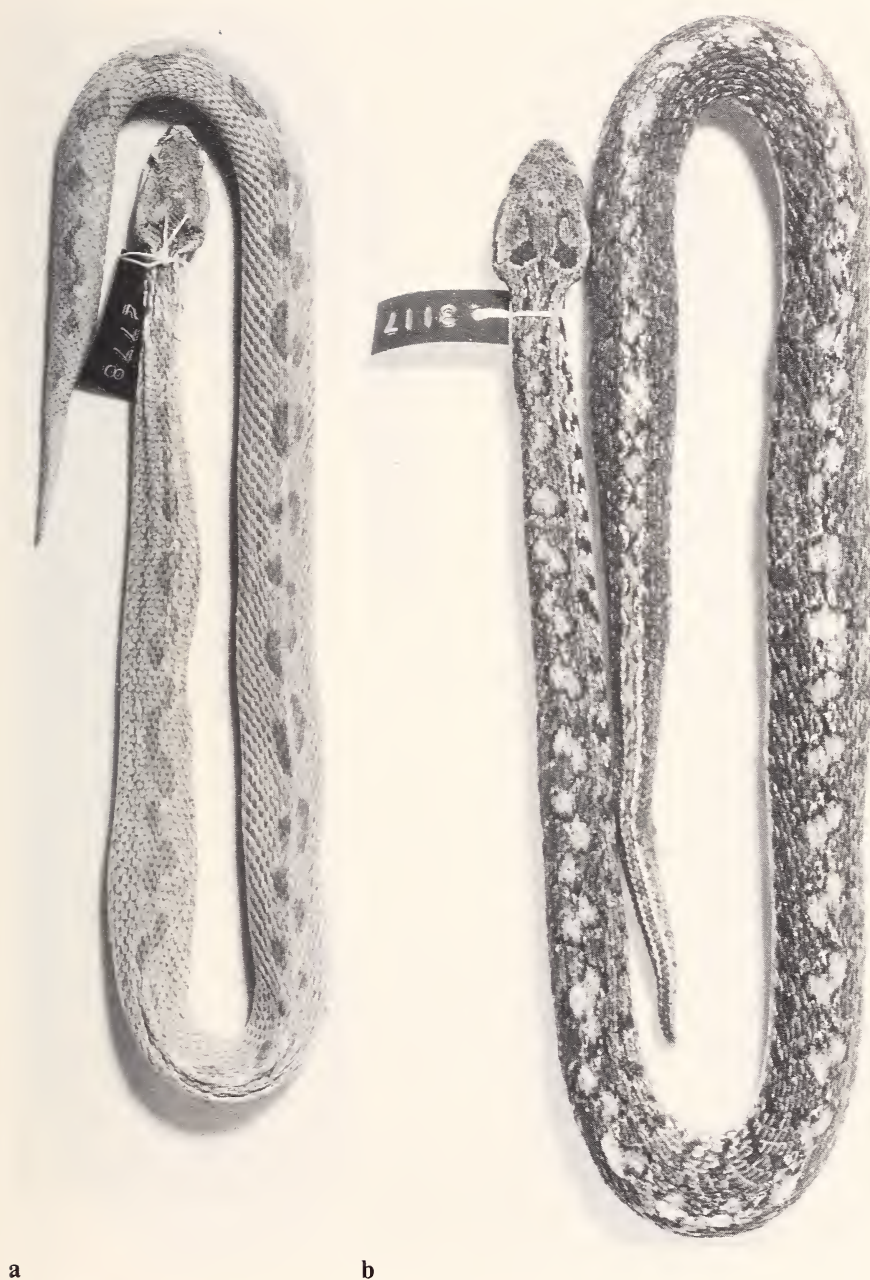


Fig. 23: Paratypes of *Vipera raddei kurdistanica* ssp. n. a) ♀ (RSI 2778) from Gotor, west Azarbaidjan; b) ♂ (RSI 3117) from Rezaeyeh, west Azarbaidjan, Iran.



Fig. 24: Paratypes of *Vipera raddei kurdistanica* ssp. n., 2 ♀, from Razi, west Azarbaidjan, Iran. (RSI 2834 and 2859).

Description (based on seven females and two males): Maximum size of females is 70.2 and of males 88.8 cm. Tail measures between 6.9 % and 7.4 % of total length in females, and between 6.4 % and 7.0 % in males.

Colour as in diagnosis. No sexual dimorphism in colour-pattern can be found in the series at hand. Very variable in colour and shape of the dorsal pattern, which can be light on dark ground colour or dark on light ground colour. The pattern can consist of a yellowish orange wavy zig-zag band with black lateral borders on a darker ground colour; smaller yellowish dark-edged spots on an almost blackish ground colour; a series of round light greyish blotches on an almost identical ground colour, which then often is dotted with very small dark spots; or having a series of dark grey irregular blotches on a very light greyish ground colour. The number of blotches along the back varies between 32 and 52 ($\bar{x} = 39.4$). Dark lateral spots are present only in the specimens with inverted colour pattern, which also is true for the dark markings on head. Belly dark in dark specimens and light and finely dotted in specimens with light ground colour.

Top of head covered with two large supraoculars, which are separated from eye by circumocular scales. The outer edge of the supraocular scales is protruding in right angle, giving the appearance of a small horn or markedly raised eyebrow. The supraoculars are separated from each other by 6 to 9 ($\bar{x} = 7.6$) interocular scales at shortest distance. Total number of intersupraocular scales is 24 to 37 ($\bar{x} = 27.5$). The number of canthals on each side separating supraocular from supranasal varies between 1.75 and 2.0 ($\bar{x} = 1.9$). 2 or 3 ($\bar{x} = 2.2$) apicals bordering rostral. The number of intercanthals is 11 to 17 ($\bar{x} = 14.3$), and with a total number of scales on top of head (intercanthals + intersupraoculars) of between 30 and 49 ($\bar{x} = 41.7$). Eye separated from supralabials by two subocular rows and surrounded by a complete first inner circumocular ring containing 12 to 17 ($\bar{x} = 14.7$) scales, and by an outer ring containing 14 to 16 ($\bar{x} = 15.4$) scales. Nostril in the middle of a big nasal shield, which is partly fused with the prenasal. Upper preocular separated from the nasal by a loreal. 9 supralabials (10 on one side in a single specimen) and 11 to 13 ($\bar{x} = 11.7$) sublabials on each side. Two large anterior chinshields followed by 4 or 5 ($\bar{x} = 4.2$) posterior chinshields. 2 to 4 ($\bar{x} = 2.9$) preventrals followed by 165 to 173 ($\bar{x} = 169.0$) ventrals in females, 172 to 178 ($\bar{x} = 174.3$) ventrals in males, and 28 to 31 ($\bar{x} = 29.4$) subcaudals in females, 32 or 33 subcaudals in males. A single anal shield. Dorsal side of body covered by 23 to 25 ($\bar{x} = 23.4$) longitudinal scale rows one head length posterior to head, 23 to 25 ($\bar{x} = 23.2$) on midbody, and 17 to 19 ($\bar{x} = 18.2$) scale rows one head length anterior to anal.

Remarks: Two specimens (RSI 2841 and 2842) from Khoi, west Azarbaijan, Iran and two specimens labeled "N.W. Azarbaijan, Iran" (BM 1976-556-7) may possibly be included in the new subspecies although more similar in trunk colour pattern to *V. r. raddei*. Groombridge (1980) who also examined the last two specimens, was of the opinion that they belong to a separated Iranian form close to *raddei*. The BM specimens are here, however, included in the nominate subspecies due to overall similarity and geographic adjacency to *V. r. raddei*.

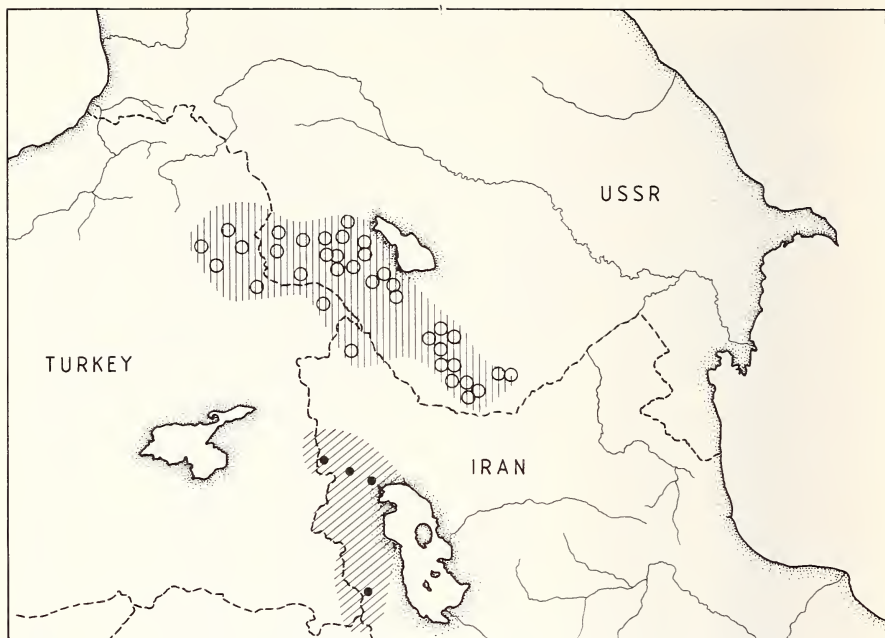


Fig. 25: Distribution map for the two subspecies of *Vipera raddei*. Known localities for *r. raddei* (open circles) and *r. kurdistanica* ssp. n. (black dots) with approximate range indicated by hatched areas.

Distribution (Fig. 25): This taxon occurs in the mountains west of Lake Urmia, along the Iranian border towards Turkey. Specimens in RSI are from Khoy, Gotar, and Razi in west Azarbaidjan in the north, and from Rezaeyeh in the south. The village Razi is situated on the Iran-Turkish border, and the taxon certainly also occurs on the Turkish side of the border, in the provinces Van and Hakkari. Further information is needed to establish the actual distribution. It is possible that the range goes further south than Rezaeyeh and also into Irak. Reed & Marx (1959) reported a viper of 60 cm length from the regions of Jaramo in northeastern Irak; and Corkill (1932) reported a bite of a horned viper, which he referred to *Cerastes cerastes*, at Dohuk (Dihok) north of Mosul in extreme northern Irak. The belief that it was a *Cerastes* has correctly been criticised by Joger (1984) on ecological and biogeographical reasons. Joger, however, thought that it must have been a *Pseudocerastes persicus* as the only possible "horned" alternative species of viper. However, as *Vipera raddei* also has pronounced raised supraoculars, which occasionally appear as "horns", it makes it a more realistic alternative species in these mountain areas of northern Irak, especially as *Pseudocerastes* and *V. raddei kurdistanica* can have the same ground colour. Moreover, the old report of a *Pseudocerastes* in the province Hakkari in southeast Turkey (Baran 1976; Joger 1984) at Yok may as well be a *V. raddei*

kurdistanica. (Joger also mentioned a second *Pseudocerastes*, deposited in BM, from the same area, at "Nohud Shak, NW of Diza", in Turkey. We have examined that specimen, labeled "Nohud Shak, NW of Diza, Persia", and which clearly was found at an Iranian locality with that name).

H a b i t a t: No information is available

R e p r o d u c t i o n: One female had 4 and a second female 9 large ova in the oviducts.

***Vipera wagneri* Nilson & Andrén, 1984**

Vipera aspis ocellata Berthold, 1850 (non *Vipera ocellata* Sonnini & Latreille, 1802)

Vipera xanthina Strauch, 1869 (part.)

Vipera raddei Nikolski, 1905 (part.)

Coluber raddei Nikolski, 1916 (part.)

T y p e l o c a l i t y: The holotype was collected by Moritz Wagner 1846 in Azarbaidjan, Iran. The collecting locality for the single known specimen was originally given as "Urmia" and "die Armenisch-Persische Grenze". The holotype (ZFMK 23495) is in the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, F. R. Germany.

D e f i n i t i o n a n d d i a g n o s i s: A species of *Vipera* within the *Vipera xanthina* species-group, thus lacking a complete circumocular ring and with the supraocular plates in broad contact with eye. Supraoculars elongate and neither raised nor with angular outer border. A single canthal scale on each side of head and two apicals in contact with rostral. A well developed rhomboid (ocellated) dark dorsal pattern along the back on a lighter ground colour. The single female differs from female *V. xanthina* in having more intercanthals, more first circumoculars, fewer



Fig. 26: *Vipera wagneri* from northwestern Iran (ZFMK 23495).

subcaudals, and only nine supralabials. It differs from female *V. bornmuelleri* in having more ventrals, a single canthal on each side, and in having fewer intersupraocular; from female *V. bulgardaghica* in having two subocular scale rows, a loreal that separates the squarish upper preocular from nasal, a higher ventral count, and a much higher number of first and second circumocular scales. The dorsal pattern is similar to that found in some female *V. xanthina* and *V. bornmuelleri*.

It differs from the *V. raddei* species-group by having supraoculars in broad contact with eye, in having a single canthal scale on each side, in lacking erected supraoculars, in a much lower number of subcaudal plates, and in a different pattern. From *V. raddei* it also differs in having a lower number of ventrals.

Description (based on the single known female): Total length of the young female is 291 mm while tail measures 21 mm (= 7.2 % of total length).

Ground colour greyish while the dorsal pattern consists of yellowish brown and more or less round blotches, surrounded by dark brown borders at anterior and posterior ends. About 24 blotches on body in the dorsal band. Two isolated oblique spots on neck, and a dark narrow band from eye to corner of mouth. Labials and side of head light in colour. Belly grey with irregularly dispatched yellowish brown blotches.

Head covered by two large supraocular plates which are in broad contact with eye and separated from each other by a row of six intercanthal scales at shortest distance. Total number of intersupraocular scales is 29. One canthal scale on each side separating supraocular and supranasal. Two apicals in contact with rostral. 29 intercanthals, with a total number of 43 small scales (intercanthals + intersupraoculars) on top of head. Eye separated from supralabials by two rows, and surrounded by a first inner circumocular ring, containing 15 and 14 scales on right and left side of head respectively. Second outer circumocular ring contains 14 and 16 scales on right and left sides. Nostril in the middle of a big nasal shield, which is partly fused with the prenasal. Upper preocular squarish and separated from nasal by a loreal shield. 9 supralabials, and 13 and 12 sublabials on right and left side respectively. Two large anterior chinshields, followed by 4 posterior chinshields. Three prefrontals, followed by 161 ventrals and a single anal. Subcaudals 24/23 on right and left side respectively. Dorsal side of body covered by 25 longitudinal scale rows one head length posterior to head, 23 on midbody, and 17 one head length anterior to anal.

Distribution (Fig. 32): The species is so far only known to occur in the province of Azarbaijan in Iran. The exact locality for the single known specimen is unknown.

Habitat: Nothing is known about the habitat for this taxon, except that the whole region is a high plateau partly covered with mountain ranges, and with peaks well above 3000 m altitude. All members of the *Vipera xanthina* complex are pronounced rock dwellers. Much of the region of easternmost Turkish Anatolia, northwestern Iran and adjacent USSR is sand and gravel semidesert and steppe areas and the species is, if it still exists, probably isolated in some limited rocky region.

Vipera xanthina (Gray, 1849)

Daboia xanthina Gray, 1849

Vipera xanthina F. Müller, 1878

Vipera lebetina Boulenger, 1896 (part.)

Vipera lebetina xanthina Werner, 1902

Vipera xanthina xanthina Mertens, 1952

Type locality: Xanthos (Kinik), restricted by Schwarz (1936). The species was described as *Daboia xanthina* by Gray (1849) based on two specimens in the British Museum (Natural History): one adult female (BM 1946.1.18.11) collected in Xanthos (Kinik), province Mugla, S. W. Turkish Anatolia (leg. C. Fellows), and one juvenile female (BM 1946.1.20.93), labeled Asia Minor (leg. A. C. Christy). The last specimen, without exact locality, was depicted by Werner (1938) as a type of *Vipera xanthina*, wrongly indicating that it was from Xanthos. For reasons of stability it becomes necessary to select the specimen from Xanthos (BM 1946.1.18.11) as lectotype.

Definition and diagnosis: A species of viper within the *Vipera xanthina* species-group, characterized by a well developed and more or less rhombic zig-zag band along the back, sharply contrasting against a light ground colour. The dorsal band contains normally less than 35 windings, rarely up to around 40, and is well



Fig. 27: Southern specimen of *Vipera xanthina*, ♀ from Ciglikara, province Antalya, Turkey (ZIG).

developed along the entire body and part of the tail. Elongated supraoculars in broad contact with eye. One canthal scale separating supraocular from supranasal. Normally 10 supralabials on each side. Eye separated from supralabials by two scale rows. Upper preocular separated from nasal by a loreal. 11 or more scales in first, and 13 or more in second circumocular ring. Interocular row of 7 or more scales. Two apicals in contact with rostral. Ventrals 148—167 in number. Females with 27 to 36 subcaudals and males with 32 to 37 subcaudals. Normally less than 14 intercanthal scales. Belly pattern with regularly dispatched larger dark blotches.

Description (based on 39 females and 29 males): Maximum size for females is 96.1 cm, and for males 96.0 cm. Tail measures between 8.4 % and 11.0 % of total length in females, and between 7.8 % and 10.9 % in males.

Ground colour varies from greyish white to brownish with a dark dorsal zig-zag pattern and smaller dark lateral spots or blotches. Males normally lighter in ground colour except in the southern populations, where females also can have a very light ground colour. Dorsal pattern often black in males and dark brownish in females, but all combinations occur and brown black-edged dorsal bands are common. Sometimes, particularly in the females, the central parts of the dorsal rhombs or windings can be yellowish brown with blackish edges. Even greenish shades occur. The areas in between the windings in the zig-zag band are often white in colour, and this is more pronounced in the northern populations and especially in females, which normally have a darker



Fig. 28: Southern specimen of *Vipera xanthina*, ♂ from Ciglikara, province Antalya, Turkey (ZIG).

lateral ground colour and more dark spots and blotches on the lateral flanks. The dorsal zig-zag band consists of 22 to 41 rhombs, blotches, or windings along the back. The mean number for the southern populations is 26.2 and for the northern populations 31.4. Neck pattern consists of two oblique spots, sometimes connected with the dorsal zig-zag band. In the southern populations 56 % of the examined specimens had one or both neck spots united with the dorsal band. The corresponding figure for the northern populations is < 16 %. Two small dots on head anterior to the oblique bands are always present. Belly pattern greyish with dark, often black half-moon shaped blotches. A dark band from posterior border of eye to corner of mouth. One or two series of alternating dark spots, blotches, or transverse bars laterally on body.



Fig. 29: Northern ♀ of *Vipera xanthina*, from Efesus, west Anatolia, Turkey (MHNG 1598,82).

Crown of head covered with two large and somewhat convex supraoculars, which are in broad contact with eye, and separated from each other by a row of 5 to 8 (\bar{x} = 6.9 for the southern populations, 6.6 for the northern) interocular scales at shortest distance. Total number of intersupraoculars 22 to 40 (\bar{x} = 30.8). One canthal scale on each side separating supraoculars and supranasals. Normally 2 apicals (\bar{x} = 2.0 in southern populations and 2.1 in northern) bordering rostral. Total number of intercanthals 7—14 (\bar{x} = 11.4 in south, 10.7 in the north) and with a total number of scales on top of head (intercanthals + intersupraoculars) ranging from 31 to 52 (\bar{x} = 42.4 in the south, 41.5 in the north). Eye separated from supralabials by two subocular rows (one row on one side of head in a single northern specimen) and surrounded by a first inner and a second outer circumocular ring containing 11—14 (\bar{x} = 12.2) and 13—17 (\bar{x} = 14.9) scales respectively. Nostril in the middle of a big nasal shield, which is partly fused with the prenasal. Upper preocular somewhat rectangular or roundish, separated from nasal by a loreal (in one specimen united with the loreal). Normally 10 supralabials on each side, but some variation occurs. Six (of 33) northern specimens have 9 supralabials on one side of head, while 4 have 11 on one side of head. In the southern populations the variation is greater. About half of the 32 examined southern specimens have diverging numbers on at least one side of head. Three specimens have 9 supralabials

on both sides, 9 specimens have 9 supralabials on one side, 15 specimens have 10 supralabials on both sides, 2 have 11 on one side, and 2 specimens have 11 on both sides. Most peculiar is the paralectotype (BM 1946.1.20.93) which has 11 on one side and 12 on the other. 8 to 14 ($\bar{x} = 12.5$) sublabials on each side. Two large anterior chinshields, followed by 4 to 6 ($\bar{x} = 4.2$) posterior chinshields. 1 to 4 ($\bar{x} = 1.9$) preventrals, followed by 147–159 ($\bar{x} = 153.4$) ventrals in southern females, 156–169 ($\bar{x} = 161.2$) in northern females, 151–159 ($\bar{x} = 155.5$) in southern males, and 158–167 ($\bar{x} = 163.5$) ventrals in northern males. A single anal shield. Subcaudals 27–32 ($\bar{x} = 29.8$) in southern females, and 27–36 ($\bar{x} = 31.2$) in northern females, 30–35 ($\bar{x} = 32.1$) in southern males, and 32–38 ($\bar{x} = 34.3$) subcaudals in northern males. Subcaudals in double rows except last spine. Dorsal side of body covered by 23 to 25 longitudinal scale rows one head length posterior to head ($\bar{x} = 23.7$ in southern *xanthina*, $\bar{x} = 23.0$ in northern *xanthina*); 23 midbody scale rows in southern *xanthina*, while in the northern populations one specimen with 21 and three specimens with 25 midbody scale rows were found (according to Boulenger 1896 and Mertens 1967 the type specimen from Xanthos, BM 1946.1.18.11, has 25 midbody scale rows, but reexamination of this holotype showed that it has only 23 midbody scale rows,



Fig. 30: A young northern ♀ of *Vipera xanthina*, from Selcuk, west Anatolia (ZIG).

in concordance with the other southern *xanthina*). The number of scale rows one head length anterior to anal varies between 17 and 19 (\bar{x} = 17.0 in the south, 17.4 in the north).

Distribution (Fig. 31): *Vipera xanthina* is distributed in the western third of Turkish Anatolia as well as in parts of Thrace and adjacent Greece. Distribution maps with exact localities have been published by Bodenheimer (1944), Baran (1976), Basoglu & Baran (1980), and by Joger (1984). Some comments must be made on these maps. Baran (1976), and Basoglu & Baran (1980) included Giyi, Alanya, at the Mediterranean coast in the distribution. This is based on Bodenheimer (1944) who reported this locality for his *V. aspis balcanica* (= *xanthina*). According to Mertens (1952) the correct locality for this specimen should be Istanbul. The specimen agrees well with the northern *xanthina* with its dark ground colour and high ventral count (160).

The locality Bolkar Dagı Ulukisla, Cilician Taurus, hints at the *V. bulgardaghica* population, which together with a specimen from Boz Dag, Ödemiş, is called *V. cf. xanthina* by Joger (1984). The Boz Dag population is, however, typical *xanthina* (Nilson & Andrén 1985 b). The easternmost known locality (according to literature, museum collections, and available observations) is in the surroundings of Ankara in central Anatolia (NMW — specimen) and at Ak Dag, north of Alanya in the Mediterranean region (Billing and Triet, pers. comm).

In the latest published map (Joger 1984) three additional localities from the eastern Taurus mountains and the region north of Syria were included. According to Joger (in litt.) the westernmost locality is Bolkar Dagı Ulukisla, mentioned by Basoglu & Baran (1980) (see above). This is, however, the same locality, based on the same specimens that Joger used when he plotted his *Vipera cf. xanthina* (= *bulgardaghica*) from Kar Boghaz, Bulgar Dagı mountains. All information about this locality and population is based on the original description of *V. bornmuelleri* by Werner (1898), in which this Bulgar Dagı population was incorporated (see Nilson & Andrén 1985 b for a more detailed discussion).

The easternmost locality mentioned by Joger (in litt.) is an inference from Werner's (1938) "Gölbaktschije", which as he inferred could be identical with a lake at about 37°N, 27°E. However, according to Werner (op. cit.) this locality should be in the southwestern part of Turkey, as Werner also had specimens (in NMW) of an endemic southwest Anatolian species of Orthoptera from the same locality. This locality is actually close to Demre, Antalya (Eiselt & Baran 1970; Basoglu & Baran 1980). We have examined the two specimens (in NMW) from this locality, and they agree in all aspects with Antalya specimens (southern *xanthina*) in having only 153 and 151 ventrals and 28 and 25 dorsal rhombs along the back.

The third eastern locality on the map of Joger is based on an observation by an entomologist visiting the region, and this information can perhaps not be rejected; yet during three different journeys to this area, we found no vipers but 10 *Coluber nummifer*, all with different dorsal patterns and some extremely similar to *xanthina* in appearance. We prefer, in this review, not to use information about distribution if no clear evidence



Fig. 31: Locality records for *Vipera xanthina*. Horizontal dashed line indicating separation line between northern and southern populations (see text).

is available, as we feel that it is easy to make wrong determinations by relying only on an observation.

Additional localities to those published by Bodenheimer (1944) and by Basoglu & Baran (1980) in Turkey are: Ak Dag, north of Alanya (Billing and Triet, pers. comm.), the ruins of Perge, prov. Antalya (own verification), Limon, new port of Antalya (own observations, ZIG), Ciglikara Ormani, about 50 km SW of Elmalı (own observations, ZIG), Ortakent, Bodrum (ZSM), Selcuk (NMB, ZIG), Efesus (NMW, MHNG, ZIG), 5 km south of Kitilbahir, prov. Canakkale, European Turkey (NMW), Ispartakule, Istanbul (Werner 1914). This species is also recorded from the Greek islands of Patmos, Lipsos, Leros, Samos, Kalymnos and Kos in the southern Sporades (Clark 1969; Pieper 1970; Schneider 1983; Grillitsch & Tiedemann, in press; Chondropoulos,

in litt; NHMB) and from the island of Symi, near Rhodos in the Dodecanese (Clark 1971). It is also reported from Chios (Ondrias 1969) and from Lesbos (Grillitsch & Tiedemann, in press). The species enters the Greek mainland in extreme northeastern Macedonia, where it is reported from Makri (Gärdenfors 1980) and close to the Turkish border (Stumpel & Strijbosch, pers. comm.).

H a b i t a t : The habitat is normally given as rocky and stony mountain slopes, often much vegetated by bushes and sometimes close to water (e.g. Eiselt & Baran 1970; Basoglu & Baran 1980; Trutnau 1975, 1981). The species also inhabits stony plains, stone walls and fences, mounds of stones, ancient ruins, maquis habitats, and meadows on rocky grounds. It has also been observed in olive groves (Gärdenfors 1980), pine (*Pinus brutia*) forests (own observations), and dolines in cedar (*Cedrus libani*) forests at high altitudes (Andrén & Nilson 1976). All observations are connected with rocky grounds. We have frequently observed it in the ancient ruin towns along the coasts of southern and western Turkey. The altitudinal span is great, from sea level to 2500 m.

R e p r o d u c t i o n : The pregnancy period for 9 different matings in captivity at the Department of Zoology, Göteborg, varied from three to four and a half months. The matings took place during March and April, and the young were born from the first part of July to the first half of August. The adults originated from Ciglikara, province Antalya, south Turkey.

The mean clutch size of the 9 clutches is 9.1 ± 1.5 SE with a range of between 2 and 15 juveniles. The mean weight in the different clutches varies between 6.33 g and 9.13 g, while the mean length in the clutches varies between 18.7 and 20.3 cm. The overall mean for all juveniles together (71) is $7.52 \text{ g} \pm 0.15$ SE and $19.7 \text{ cm} \pm 0.10$ SE for weight and length respectively. Minimum and maximum values in weight are 5.63 and 9.81 g, and in length 17.8 and 21.1 cm.

KEY TO THE SPECIES IN THE *XANTHINA* COMPLEX

- 1 a Elongated supraoculars in broad contact with eye; one (or rarely one and a half) canthal scales between supraocular and supranasal on each side of head; body more stocky 2
- 1 b Outer border of elongated supraoculars angular and raised; supraoculars separated from eye by a row of small scales; two or more canthal scales separating supraocular and supranasal on each side of head; body slender 7
- 2 a Normally one subocular row of scales between eye and supralabials; upper preocular elongated, in contact with nasal or nearly so; 9–11 scales in first and 10–13 in second circumocular ring; interocular row of 6 scales; often three apicals in contact with rostral; nine supralabials; tip of tail red in life, "bridle" across snout; dorsal pattern of 40–46 blotches of zig-zag windings. Distribution: south central Anatolia *Vipera bulgardaghica*
- 2 b Two subocular rows between eye and supralabials; upper preocular of variable size but separated from nasal by a loreal; 11 or more scales in first, and 13 or more scales in second circumocular ring; interocular row of 7 or more scales; tip of tail yellowish 3
- 3 a Pattern reduced and normally fragmented, more than 47 dorsal irregular transverse bands; less than 153 ventrals; females with 27 or less subcaudals, males with 31 or less subcaudals; often three apicals in contact with rostral; 9 supralabials on each side; 30 or more intersupraoculars; belly pattern normally unicoloured or finely dotted 4
- 3 b Dorsal pattern consisting of less than 41 rhomboid blotches or zig-zag windings; more than 147 ventrals; two apicals in contact with rostral; nine or ten supralabials. Distribution: Turkey, Iran 5
- 4 a Tendency towards sexual dimorphism in pattern: females with retained juvenile pattern (Fig. 5 D), males with fragmented pattern; normally small body size (< 55 cm); 6–8 ($\bar{x} = 7.1$) interoculars separating supraoculars; 21 or 23 ($\bar{x} = 22.1$) midbody scale rows and 17 or less scale rows (in half of the specimens) on posterior part of body; 6, or more rarely 4 ($\bar{x} = 5.2$) posterior (second) chinshields. Distribution: Mt. Liban in Lebanon *Vipera bornmuelleri* (Mt. Liban populations)
- 4 b Both sexes with fragmented pattern; large body size (max. size around 75 cm); 8–9 ($\bar{x} = 8.3$) interoculars separating supraoculars; 23 midbody scale rows and 17 scale rows on posterior part of body; four posterior (second) chinshields. Distribution: Mt. Hermon in Syria (and Israel administered area) *Vipera bornmuelleri* (Mt. Hermon populations)
- 5 a Females with around 23 subcaudals and 161 ventrals; 9 supralabials on each side; around 14 intercanthal scales; around 29 scales in first circumocular rings (counted on both sides together); less than 30 intersupraoculars; belly pattern with irregularly dispatched brownish blotches. Distribution: northwestern Iran *Vipera wagneri*
- 5 b Females with 27 or more subcaudals and males with 32 or more subcaudals; 10 supralabials on each side of head; normally less than 14 intercanthal scales; 28 or less scales in first circumocular rings (counted on both sides together); belly pattern with regularly dispatched, large dark blotches. Distribution: western half of Turkey, easternmost Greece 6
- 6 a Between 147 and 159 ventrals ($\bar{x} = 154$); pattern consisting of 24–30 ($\bar{x} = 26$) united blotches or zig-zag windings; neck pattern often united with dorsal pattern ($> 50\%$); ground colour normally light grey in both sexes; reduced white colour between zig-zag windings. Distribution: southwestern Anatolia *Vipera xanthina* (southern populations)
- 6 b Between 158 and 167 ventrals ($\bar{x} = 162$); pattern consisting of 28–41 ($\bar{x} = 31$) united blotches or zig-zag windings; neck pattern less often united with dorsal pattern ($< 16\%$); ground colour often darker and marbled in females; pronounced white colour between zig-zag windings. Distribution: western and central Anatolia, Istanbul area, and easternmost Greece *Vipera xanthina* (northern populations)

- 7a Relatively short tail (less than 8 % of total length in both sexes); normally more than 170 ventrals in males and more than 165 in females; normally 34 or less subcaudals in males; dorsal pattern inverted (lighter reddish or yellowish pattern on dark ground colour) or normal but much reduced. Distribution: Armenian USSR, eastern Turkey, northwestern Iran ... 8
- 7b Relatively long tail (normally 8 % or more of total length in both sexes); normally less than 170 ventrals in males and 166 or less in females; normally 34 or more subcaudals in males; pattern normal (dark pattern on light ground colour) but may be much reduced. Distribution: northern Iran 9
- 8a Monomorphic in colour pattern (pattern inverted); neck pattern lyrate or consisting of pronounced oblique or transverse streaks; body ground colour dark. Distribution: Armenian USSR, eastern Turkey and northwestern Azarbaidjan, Iran *Vipera raddei raddei*
- 8b Polymorphic in colour pattern (pattern inverted, unicoloured or normal); neck pattern sometimes absent; ground colour variable, often light. Distribution: western Azarbaidjan, Iran, perhaps also adjacent parts of Turkey and extreme northeastern Irak *Vipera raddei kurdistanica*
- 9a Monomorphic in colour pattern with well developed black-edged dorsal zig-zag band, and black drop-like oblique spots on nape; pale dark-edged supraoculars; two apicals in contact with rostral. Distribution: northern Iran *Vipera albicornuta*
- 9b Polymorphic in colour pattern with dorsal pattern more or less reduced consisting of zig-zag band, blotches, vertebral stripe or totally lacking; with or without two oblique streaks on nape; supraoculars not pale and dark-edged; often three apicals in contact with rostral. Distribution: northern Iran (central Albours mountain range) *Vipera latifii*

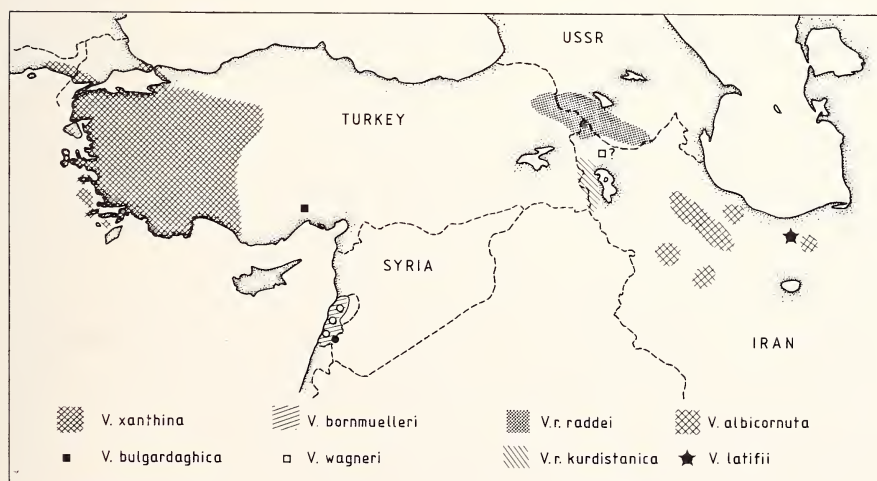


Fig. 32: Distribution map for the species in the *Vipera xanthina* complex. For *Vipera bornmuelleri* open circles indicate the Mt. Liban populations, while dark dot is the Mt. Hermon population.

PHYLOGENETIC RELATIONSHIPS

The morphological characters investigated have been examined and evaluated for their phylogenetic information content. A hypothetical phylogeny of the included taxa has been constructed (Table 6; Fig. 33), based on the data presented earlier in this paper. These data have been subjected to a cladistic analysis, following the principles of Hennig (1966). Only the relatively apomorphic (derived) state of a given character has been used as evidence of phylogenetic relationship. It has not always been assumed that taxa sharing apomorphic morphometric characters are closely related. In fact, the distribution of some character states among taxa indicates that the shared possession of apomorphies for these characters is a result not of common ancestry, but rather of parallelism. An increased number of second chinshields that occurs in the Mt. Liban population of *bornmuelleri* and in *latifii*; three instead of two apicals in contact with rostral that occurs in *bulgardaghica*, *bornmuelleri*, and *latifii*; as well as the pronounced

Table 6: List of taxa exhibiting derived character states in the *Vipera xanthina* complex

Derived character	Taxa
1. increased number of crown scales	<i>bornmuelleri</i>
2. increased number of canthals	<i>raddei</i> species-group
3. three apicals	<i>bulgardaghica</i> , <i>bornmuelleri</i> , <i>latifii</i>
4. angular supraoculars	<i>raddei</i> species-group
5. short upper preocular	all except <i>bulgardaghica</i>
6. complete circumocular ring	<i>raddei</i> species-group
7. many first circumoculars	all except <i>bulgardaghica</i>
8. many second circumoculars	all except <i>bulgardaghica</i>
9. double subocular row	all except <i>bulgardaghica</i>
10. increased no. of supralabials	<i>xanthina</i>
11. increased no. of sublabials	<i>xanthina</i> , <i>wagneri</i>
12. many second chinshields	<i>bornmuelleri</i> (Mt. Liban), <i>latifii</i>
13. few midbody scale rows	<i>bornmuelleri</i> (Mt. Liban)
14. few posterior scale rows	<i>bornmuelleri</i> (Mt. Liban)
15. increased no. of preentrals	<i>wagneri</i> , <i>r. raddei</i> , <i>r. kurdistanica</i>
16. increased no. of ventrals	all except <i>bulgardaghica</i> and <i>bornmuelleri</i>
17. increased no. of subcaudals	a) <i>xanthina</i> , <i>raddei</i> species-group b) <i>albicornuta</i> , <i>latifii</i>
18. relatively short tail	<i>r. raddei</i> , <i>r. kurdistanica</i>
19. reduced dorsal pattern	<i>r. kurdistanica</i> , <i>latifii</i>
20. inverted pattern	<i>r. raddei</i>
21. division of rhombs	<i>bornmuelleri</i>

reduction of dorsal pattern that can be seen in *bornmuelleri*, *raddei kurdistanica*, and *latifii*, are all examples of multiple origin of derived characters. The evolution of such a character in this group of vipers is more likely to be a response to selection in similar narrow adaptive zones such as small isolated mountain valleys. Such cases of parallelism and convergence are included in the cladogram (with underlined numbers). All morphometric characters that are common for the whole complex or vary in a true clinal fashion without gaps are omitted from the phylogenetic analysis. Some of the investigated characters, such as total length, are not used either.

The taxa in the *xanthina* species-group phenetically represent a sister group of the *raddei* species-group, mainly on the basis of head morphology as they all have supraoculars in broad contact with the eye and dividing the circumocular ring, and a pronounced dorsal pattern. Cladistically, however, only *V. xanthina* constitutes a plesiomorphic sister group to the *raddei* species-group, as the remaining taxa in the *xanthina* species-group show a pectinate branching from the main stem (Fig. 33).

The three species *bulgardaghica*, *bornmuelleri*, and *wagneri* have a low number of subcaudals, which is probably a symplesiomorphy. *Vipera bulgardaghica* and *V. bornmuelleri* further share a low ventral number, which is also a plesiomorphic state, and they share having three apicals in contact with rostral, an apomorphy that probably evolved through parallelism and is not found in the single *V. wagneri*.

Conspicuous autapomorphies are more common within the *xanthina* species-group than in the *raddei* group, which may indicate older age of the taxa in the former assemblage. The restricted and probably relictual distribution of *wagneri* and *bulgardaghica* would fit in with that idea. The latter species seems to be unique in its reduced head scalation. *Vipera bornmuelleri* and *V. wagneri* have a similar reduced number of subcaudals as in *bulgardaghica*, but they both have the synapomorphic lateral head scalation that causes them to resemble *xanthina*. Even so, they have the same type of dorsal pattern, which however is lighter than in *xanthina* and is, in *bornmuelleri* at least, much reduced in the adult stage.

The eastern taxa (*r. raddei*, *r. kurdistanica*, *albicornuta*, and *latifii*) clearly constitute a monophyletic group united by several synapomorphies, such as the supraocular shape, the closed circumocular ring, and the canthal numbers. As shown by Groombridge (1980) they also share a similar aberrant form of maxilla. *Vipera latifii* and *V. albicornuta* are also a monophyletic group characterized by a high subcaudal count.

The reduction of the dorsal pattern is probably an apomorphy that has been expressed to different degrees in the different taxa of the *raddei* group through parallelism, resulting in the development of autapomorphic patterns in *latifii* and *r. kurdistanica*. The Armenian populations of *raddei* with inverted pattern, which have dorsal markings less sharply demarcated due to loss of dark borders, represent still another expression of this trend towards loss of an original prominent blotched or zig-zag pattern. *Vipera latifii* has the most apomorphic pattern in this group with its marked polymorphism. It is the only species that can completely lack dorsal blotches. The occurrence of a vague zig-zag band in many specimens of *latifii* probably represents the remnants of

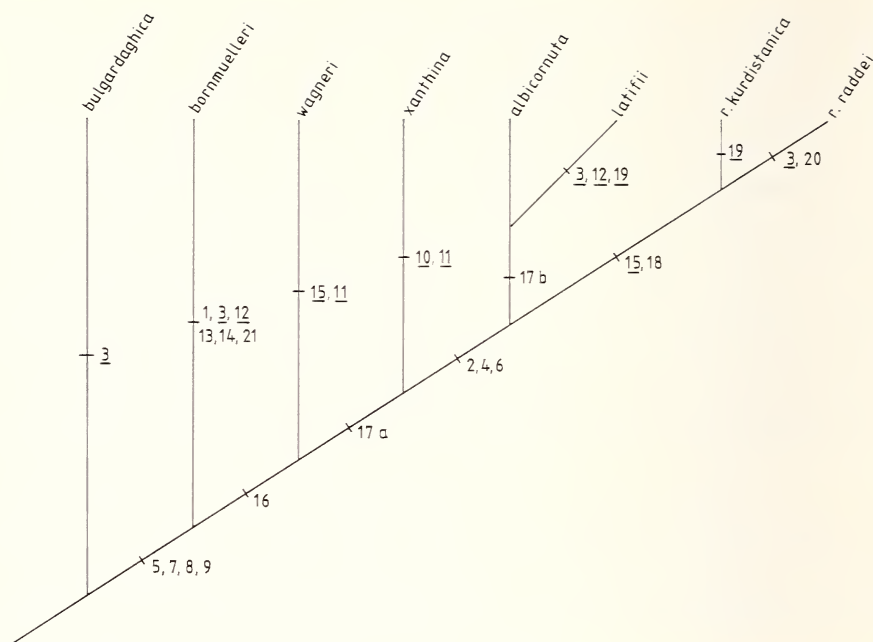


Fig. 33: A theory of phylogenetic relationships among the taxa of the *Vipera xanthina* complex. Numbers refer to derived character states listed in Table 6. Underlined numbers mark identical shifts (convergence) in character states.

an ancient well-developed zig-zag pattern. The only species in the *raddei* species-group that has retained a well developed dark-edged zig-zag band is *albicornuta*. In this character, it is similar to (the geographically close) *V. wagneri* as well as to the rest of the *xanthina* species-group, and this state may be interpreted as a plesiomorphy.

The branching sequence in the evolutionary history of the different species in the paraphyletic *xanthina* species-group, according to the different apomorphic patterns and degree of overall differences between taxa and groups, seems to have occurred in a stepwise way. Without fossil remains, it must be quite hypothetical to speculate on ancestral forms; but the monophyletic *raddei* group may have evolved from a common ancestral form of the *xanthina* stem somewhere in the northern regions of the Iranian plateau.

The question then arises whether the *xanthina* complex as a whole is a monophyletic group, and what the relations are to other groups of advanced vipers of genus *Vipera* (*lebetina* and *russelli* complexes). These larger vipers share a number of synapomorphic characters such as increased number of dorsal scale rows, increased number of subcaudals, increased number of subocular scale rows, size etc., and must be considered as a more derived branch of vipers. At the same time, they seem to be a much older group as suggested by their zoogeographic pattern, occurring from Morocco

(*mauritana*) to Indonesia (*limitis*) and Taiwan (*formosensis*), and by the fossil records (see next section), while the *xanthina* complex is of younger evolutionary origin (restricted distribution, continuous rapid speciation and radiation, distribution pattern in relation to paleogeography, etc). The *lebetina-russelli* stem seems to be phenetically most similar to the *xanthina* species-group. A likely pattern is that a "pre-*xanthina*" branched off from the main stem some time during the Tertiary period, remained in a small and isolated area somewhere in the Middle East, and started to radiate first at the end of the Tertiary period and during the Quaternary period, with the formation of the present pattern. Members of the *xanthina* species-group and the *lebetina* stem (s. lat.) are similar in many characters, such as ventral numbers and supraocular (when not fragmented) in contact with eye, and a partly parallel evolution since the separation from the common ancestor (which may have had some similarities with the most original members of the *xanthina* species-group) must be assumed. There are, however, no obvious synapomorphies that unite the *xanthina* species-group, or any other grouping in the *xanthina* complex, with the *lebetina* complex s. lat. The *xanthina* complex is morphologically most similar to the *palaestinae-russelli* branch (of the *lebetina* stem) through several symplesiomorphies (presence of supraoculars, pronounced dorsal pattern, low number of canthals and apicals) and it is perhaps reasonable to assume that the *xanthina* complex originated from this branch of advanced vipers.

No clearly synapomorphic morphological characters have been found for the whole *xanthina* complex [although several ecological ones have, such as habitat choice (high altitude rock dwellers) and reproduction (ovoviparous; most *lebetina* populations and *palaestinae* are oviparous)] which therefore must be considered as paraphyletic. Thus, the branching off from the *lebetina* stem (s. lat.), with the *xanthina* species-group as intermediate between an ancestor and the *raddei* species-group, must at this stage be hypothetical.

THEORIES OF EVOLUTIONARY PATTERNS

The present taxonomic diversity is a result of the past geological and climatological changes in the eastern Mediterranean area and the Middle East. Parts of the region have gone through extensive climatological oscillations, especially during the Pleistocene, with five ice ages and four interglacial periods with periodically warm climate. Contemporary binding of the sea waters in continental glaciers had an influence on the sea level, with periodically exposed large land masses that are part of the Mediterranean sea today.

The members of the *xanthina* complex are all stenotopic, restricted to rocky habitats. The present ranges of the different taxa probably originate from once continuous distributions which today are fragmented, primarily due to climatological and geological changes. Large mountain zones have moulded into gravel hills and semi-deserts over large areas in the Near and Middle East, leaving relict populations in remnant rocky areas and patches. Inability to adapt to moulding biotopes has effectively isolated such

populations. *Vipera bulgardaghica* in Cilician Taurus and *V. wagneri* in northwest Iran are probably examples of such small, isolated, and perhaps now extinct populations. Other similar fragmented populations might have existed until recent times or might still be expected to occur in eastern Turkey, Iran and northern Iraq. According to several authors (see Szyndlar 1984 for review) a great modernization of the Holarctic snake fauna, with the formation of modern ophidian taxa, took place during the Miocene epoch. The Pliocene is considered as a transitional period in which many extinct snake species were replaced by the present forms, while in the early Pleistocene exclusively recent species, although osteologically somewhat different from modern taxa, existed (Szyndlar 1984).

In North America the modern snake species are not known before the upper Pliocene (Holman 1979). Pliocene and Pleistocene fossil records suggest that most modern species of rattlesnakes (*Crotalus*) had differentiated and attained their present ranges by the middle or late Pliocene (Brattstrom 1964). The oldest *Vipera* fossils are from the Miocene of Europe (Szyndlar 1984; Bolkey 1913) and, if the paleontological patterns of rattlesnakes were contemporary with the differentiation of modern vipers, many of the vipers in the Middle East, including the *xanthina* complex, could have reached their present form well before the Pleistocene, with its cyclic pattern in climate.

The modern snake faunas of Europe were mainly formed by immigrants from the east that invaded the continent from Asia Minor during the Pliocene. The present systematic pattern of the *xanthina* complex probably started to differentiate already during this period, at least concerning the main lines. Considering the taxonomic relationship and present distributions, the origin of at least some taxonomic levels (subgroups, subspecies, and some species) resulted from local speciation, owing to rapid isolations that were usual in fluctuation conditions at the end of the Pliocene and during the Pleistocene.

If we look at the present taxa in the group, different degrees of microevolution must have continued during the Quaternary period with its different periods of glaciation. The Pleistocene period that lasted for about 1.6 million years, with its glaciations with intervening interglacials, markedly changed the climate and sea level in these parts of the Near and Middle East. This, of course, caused opportunities for racial differentiation or further speciation in many taxa. The different microraces in the *xanthina* complex as seen today (northern and southern *xanthina*; Mt. Liban and Mt. Hermon *bornmuelleri*) as well as newly differentiated subspecies and species (*r. raddei* and *r. kurdistanica*; *albicornuta* and *latifii*) probably evolved during the Pleistocene with its fluctuating climate. Populations must have become isolated in glacial refugia a number of times, and in many cases this resulted in new lines, especially as a partly severe climate exterminated remaining populations over large areas.

Vipera wagneri may also be a relict from this period, which has survived in a refugium until the present, far away from the *xanthina* species-group. This vicarian explanation is verified by a number of other species of reptiles, such as *Lacerta parva*, *Eremias suphani*, *Telexcopus fallax iberus*, *Erys jaculus familiaris* etc., which all show this divided distribution.

An understanding of the present distributional pattern of *Vipera xanthina* can be obtained by analysing the historical zoogeographic patterns of vipers in the east Mediterranean region. *Vipera lebetina*, which is related to the *xanthina* complex, is a large species of probably old origin (Wettstein 1953) which is partly sympatric with members of the *xanthina* complex, although always ecologically separated in being a steppe inhabitant in all areas of coexistence. The species is probably of much older origin than *xanthina* in western Anatolia, and seems to have been preceded by an ancestral form of larger size than nowadays. Generally, the Plio-Pleistocene herpetofauna of Europe and adjacent areas consisted of ancestral taxa of much larger size than their present descendants (Bolkay 1913). Remnants of such a large viper have been found on the island of Chios (where *xanthina* occurs today) in the Aegean Sea, from the middle Pleistocene (Schneider 1975). These remnants, which consist of fossil vertebrae (NMF, reexamined by us), are very similar in size and form to vertebrae from large specimens (ZIG) of the recent *V. l. lebetina* from Cyprus. This taxon is certainly of old age and reached a wider distribution in the Aegean region, as well as large parts of southern Europe, already during the Miocene and Pliocene, in periods with land connections to northern Africa (via the Tyrrhenis) and when the Aegean Sea and larger parts of the adjacent Mediterranean were dry. Fossil remains of such a *lebetina* have been found in Villafranchian of Spain, and the existence of *lebetina* in the whole of southern Europe during the Miocene and Pliocene has been postulated (Saint Girons 1980). The present distribution of *lebetina* in the Mediterranean is restricted to the wellknown localities in Cyprus, adjacent Turkey, Syria, Lebanon, and the Aegean Cyclades, but also to the coastal region of Algeria (BM, USNM specimens), which is a distribution that can be explained by vicariance models. The Cyprus population (*l. lebetina*) became isolated from Syria in the late Pliocene or early Pleistocene (Haas 1952), but has changed little compared to recent south Anatolian, Syrian, and Algerian populations, indicating that the ancestral *lebetina* form is very similar to the recent one. The other north African populations (*mauritanica* group) must have been separated from the recent *lebetina* stock much earlier. An ancestral form (*Vipera maghrebiana*) has been described from the middle Miocene in Morocco (Rage 1976).

The Milos area in the Aegean Sea was isolated already during the Plio-Pleistocene (Greuter 1970) and today we find a small form of *lebetina* (*schweizeri*) on that group of islands, which must have differentiated from the ancestral larger form during roughly the last million years. Although much smaller, it still has the same number of ventrals as the larger *V. l. lebetina* and adjacent populations of *V.l. obtusa*. This may be an indication of a retrogressive evolution in *Vipera* (Saint Girons 1978).

The dry-steppe-inhabiting *lebetina* must, during the climatological fluctuations that took place in the Pleistocene (with pronounced glaciations also in parts of Anatolia), have retreated from a large part of its western ranges, leaving the remnant populations in the Aegean Sea and in Algeria as the only survivors to the present. The species has a mainly Middle East occurrence today. Also the large Chios form certainly became extinct during some Pleistocene cold period (Würm?) when much of the northeastern Mediterranean region was forested (Butzer 1958).

Some time during the Pleistocene the climatic conditions together with the disappearance of the possible competitor (*V. lebetina*) allowed the much more cold-tolerant *xanthina* to spread north and west from some refuges, and today the whole central and parts of the western and southern shores of Anatolia are inhabited by *xanthina*. The western border for this taxon reaches the whole Turkish Aegean coastline, as well as most of the islands that were connected with Anatolia during the early Pleistocene (including Chios). Thus *xanthina* spread west to the Pleistocene shores of Anatolia, but was too late to be able to spread further into the Aegean Sea (where *lebetina* had been isolated much earlier). Today *Vipera xanthina* occurs on the islands of Lesbos, Chios, Samos, Kalymnos, Kos, Patmos, Simi, Leros, and Lipsos which are all close to the Anatolian coast and were part of the Anatolian mainland during the Pleistocene (Greuter 1970).

Further north, however, *xanthina* spread through the land bridges that existed for longer times (Erol 1976), across the Bosphorus and Dardanelles into mainland Europe, where it has been found in the Istanbul area (Werner 1914), southern Thrace (NMW-specimen), and the northeastern corner of Greece (Gärdenfors 1980). This is a similar zoogeographical pattern to that found in *Ophisops elegans* and *Agama stellio* (Wettstein 1953).

During the Pleistocene glacial periods, when large areas of central Europe and the Caucasus were covered with ice, the climate of adjacent areas of the northern part of the Mediterranean Sea and in Asia Minor was first of an alpine or subalpine character (Hammond 1976), adverse for poikilothermal terrestrial vertebrates. Molluscs of boreal waters such as *Arctica islandica* and *Panomya norvegica* occurred in the Mediterranean, and fossil bones of the Great Auk (*Alca impennis*) have been found in southern Italy from this period (Pfannenstiel 1954). Those areas of the Near and Middle East that were not of alpine character were forested by deciduous, mixed, or pine forests of a kind found in more northern parts of Europe and Asia today (Butzer 1958; Zohary 1973).

Thus, the *lebetina* form withdrew from the western range during these periods of cold, while an ancestral form of the present *xanthina* could well have survived in one or several refuges in Asia Minor or adjacent Asia. *Vipera xanthina* occurs today in some different habitats, ranging from sea level to 2500 m altitude, in rocky habitats which often have a forest influence. It is well known from the typical Mediterranean maquis (phrygana) biotopes, but this is not an original plant community in many areas and the species probably occurred primarily in more open forest habitats. We have found the species in pine forests (*Pinus brutia*) at sea level close to Antalya, as well as in subalpine cedar forests (*Cedrus libani*) in the Elmalı region (Ciglikara) at about 2000 m altitude. The wide ecological amplitude of this species certainly enabled it to survive at least in some Pleistocene forest refuges. It is, of course, reasonable to guess that such refuges for *xanthina* were more southern than the range of the species is today, but without fossil remains nothing can be postulated about this. The morphological differences between *xanthina*, *bulgurdaghica*, and *bornmuelleri* suggest, however, that all three taxa were separated much earlier than during the ice ages of the Pleistocene,

even if a rapid evolution of different population groups of a "pre-*xanthina*" towards speciation must be considered.

At least two different refuge areas of *xanthina* populations seem to have existed during the Pleistocene. The difference in pattern, colour, and ventral count of the southern populations compared to the more northern, central, and west Anatolian populations may be a result of isolation due to climatological barriers during the Pleistocene. A similar pattern is found in many other groups of reptiles and amphibians in parts of southwestern Anatolia today, with a separation on species or subspecies level (e. g. *Mertensiella luschani*, *Blanus strauchi bedriagae*, *Ophiomorus punctatissimus*, *Lacerta danfordi pelasgiana*, *Vipera ursinii anatolica* etc.) indicating a united refuge in this corner of Anatolia. This region is also inhabited by endemic mammalian taxa such as *Dryomys laniger* (Gliridae) as well as several endemic plants (Zohary 1973). This area might have served as a refuge for several reptiles and amphibians for very long periods of time, as *Mertensiella* also occur on Karpathos which was separated from Anatolia (Aegean Arch) during the Pliocene. The more northern populations of *xanthina* perhaps survived in a series of younger refuges separated from each other mainly during the last glaciation (Würm), which could explain the smaller morphological differences that exist between the local populations.

The differentiation of the four species in the *xanthina* species-group is, of course, of older origin. Again, lack of fossil remains must make this part of the discussion hypothetical, but there is some evidence of an originally more southern extension and refuge also for taxa on this level.

Parts of the Taurus mountains such as Bulgar Dagh in Cilician Taurus, were glaciated during the Pleistocene (Louis 1944), and the isolated *Vipera bulgardaghica* either reached this mountain chain from some southern area or, more probably, "hibernated" in some lowland refuge in the region. There also are some indications that *bulgardaghica*, which so far has only been recorded from this single locality, has been effectively isolated for a considerable period of time. This locality also is inhabited by the endemic frog, *Rana holtzi*, a good species related to *Rana macrocnemis*, which is partly sympatric with *V. xanthina* in western Turkey and with *V. latifii* in northern Iran (in a different habitat, through *R.m. pseudodalmatina*), and to *Rana camerani*, which is sympatric with *V. raddei* in eastern Turkey and in USSR. *Rana camerani* does also occur in northeastern Iraq (Kevork 1972) which is a possible range for *V. raddei kurdistanica*. Specimens of *Coluber ravergieri* s. str., which also has an isolated occurrence on Mt. Hermon (Hoofien 1968; Schätti & Agasian 1985), have also been collected by us (ZIG) at 2,300 m altitude in the Bulgar Dagh area. The clear pattern of endemism in the Bulgar Dagh area shows that this locality, and *V. bulgardaghica*, have been effectively isolated, perhaps during a similar or even longer period of time than *bornmuelleri* in Lebanon-Syria, and thus forming the phylogenetically most original taxon in the group. Parts of these mountains of inner Anatolia and the Lebanon mountains have, geobotanically, been very stable and persisted without much changes since the Miocene (Zohary 1973). According to Picard (1937, 1943) there has been a climatic stability in this region since the Mio-Pliocene. Analysis of Pleistocene

pollen has shown that the same trees that presently occur in the mountains of Lebanon and Mt. Hermon occurred in northern Israel during the Pleistocene (Lorch 1959). Fossil rodent and bird faunas from the lower Pleistocene contained typical Mediterranean elements (Zohary 1973). The general picture is that no marked climatic changes occurred in this region during the entire Pleistocene.

Thus *V. bornmuelleri* probably occurred in the Lebanon area during the whole Pleistocene. Many reptiles that occur on Mt. Hermon today clearly have an Anatolian affinity (Haas 1952; Hoofien 1968, 1973; Zinner 1972) and this corner of the Mediterranean region has probably served as an original refuge for many Anatolian faunal elements. Many other animals and plants which presently have a more northern distribution also occur as isolated relicts in the Mt. Hermon region, either as isolated populations or subspecies of widely distributed species or as close relatives. Taxa with similar distribution to *bornmuelleri* versus the rest of the *xanthina* species-group are *Eirenis modestus*, *Telescopus fallax*, *Coluber nummifer*, *Elaphe quatuorlineata sauromates*, and *Elaphe hohenackeri*.

The present distribution of *xanthina* is thus partly explained by dispersal hypotheses. The occurrence of *lebetina* in Pleistocene west Anatolia is evidence that *xanthina* was lacking, as the two species never are sympatric (which may depend on competition), and that the climate was much drier. However, the present distribution pattern of the entire *xanthina* species-group may also be tested as to the vicariance hypothesis. Another monophyletic group of reptiles, the archaeolacertan lizards of the *Lacerta danfordi* group, has a similar distribution (Basoglu & Baran 1977; Arnold 1972). *Lacerta d. danfordi* occurs in the Cilician Taurus in the same region as *V. bulgardaghica*, and geographically separated from its west Anatolian subspecies in an identical pattern as *bulgardaghica* is from *xanthina*. The south *xanthina* populations are sympatric (in the same microhabitat) with *Lacerta danfordi pelasgiana*, while the northern *xanthina* is sympatric with *L. danfordi anatolica*. *Vipera bornmuelleri* is sympatric with *L. danfordi kulzeri* on Mt. Liban (Hoofien 1968) and with *Lacerta laevis*, which is the closest relative to *L. danfordi*. *Lacerta laevis* and *L. d. danfordi* are sympatric in the regions from Lebanon to Cilician Taurus in Turkey, which shows that these species have dispersed after speciation took place. *Lacerta laevis* also occurs on Cyprus which suggests, if this four-area pattern is accepted as evidence for the vicariance model of the speciation pattern in the *xanthina* group, that *bornmuelleri* was isolated and started to differentiate before the late Pliocene and early Pleistocene, when Cyprus became isolated from Syria.

Lacerta parva, which has a sympatric distribution with *Vipera xanthina* and *V. bulgardaghica* (but in different microhabitats) and probably with *V. wagneri* (and the *raddei* species-group), has a close relative in *Lacerta fraasi* which is sympatric with *V. bornmuelleri* in high Lebanon. Central Anatolian *L. parva* seem more primitive compared to Armenian *L. parva* (Peters 1962), indicating that this species has also invaded the Armenian region from central Anatolia, with concordant isolations due to Pleistocene climatic shifts. This may be a parallel case to the paleontological history and distribution pattern of *V. wagneri*, which has its probable origin in more west

Anatolian "pre-*xanthina*" populations, and as such giving evidence of a vicariance model of differentiation (Wagner 1868, 1889; Platnik & Nelson 1977).

Thus the region of Mt. Hermon, and adjacent areas further north, seems to have been one main refuge for an ancestral form of the *xanthina* species-group. *Vipera bornmuelleri* and *V. bulgardaghica* have very low numbers of ventrals, and this is considered as a primitive and original condition in *Vipera* (Saint Girons 1978) and in Colubroidea in general (Marx & Rabb 1972); and this supports the hypothesis of *bulgardaghica* and *bornmuelleri* as being most ancient in the *xanthina* species-group. Some populations of a hypothetical ancestral form may have remained, and performed altitudinal movements with fluctuating climate. *Vipera bulgardaghica* might have been such a case. Some populations may have evolved into the modern *bornmuelleri*, while other branches of the original ancestor spread north into secondary refuges in Lycia (south *xanthina*), the Aegean part of Anatolia, or Phrygia (north *xanthina*) and an eastern branch towards Azarbaijan in Iran (*wagneri*) already during the Pliocene. In the last case, it might just as well be that *V. wagneri*, with morphological similarities both to *bornmuelleri* and to *xanthina*, represents a reminiscence of a connection with the eastern *raddei* species-group, and thus supports the idea that the differentiation of the *raddei* branch from the *xanthina* stem is of more eastern origin.

The region of Armenia, where *V. raddei* has its present distribution, had a much colder climate during the Pleistocene glacial periods. Both during the Riss (200,000—230,000 years ago) and during the Würm (30—65,000 years ago), the Caucasus region became cold and glaciated, and *raddei* probably had its total refuge much further south, perhaps in the region where *kurdistanica* occurs today. This latter subspecies is extremely polymorphic in trunk pattern, and also the inverted reversed colour pattern morph that is typical for all *r. raddei* can be found in the *r. kurdistanica* populations, indicating a secondary contact, perhaps during the Würm, and indicating that a more or less continuous gene flow may have taken place between the population groups. Anyhow, the northern *r. raddei* probably originated from some ancestral form close to *r. kurdistanica*. Transcaucasia is often referred to as a major center for speciation for palearctic forms (e. g. Yablokov et al. 1980), and the original branching of the *raddei* stem from *xanthina* might have occurred here, especially as *V. wagneri* of the *xanthina* stem still exists in the region as a living evidence of this hypothesis. The climatic shifts during younger geological times have, however, forced *raddei* to move in a north — south direction and thus created secondary refuges in Iranian Azarbaijan where *r. kurdistanica* occurs today.

Also the Alburz mountains, the known range for *latifii*, and the mountain ridges further south and west where *albicornuta* is found, may have been refuges during the Pleistocene, with populations still remaining. These regions have been very stable for a considerable time, and the recent flora (with many endemics) is very similar to that from the upper Miocene (Sitar 1964). During the Pleistocene, the snow line in northern Iran dropped 1,000 m below the present level (Melchior 1937). The glaciers were restricted to the northern slopes of the Alburz mountains. The rainfall conditions in inner Iran during the Pleistocene were not very different from those today, and the

absence of glaciers on the southern Alburz slopes was due to drought. This suggests that the more southwestern Zanzan mountains and adjacent areas were original refuges and perhaps a center of origin of the *albicornuta-latifii* stem.

Again, the isolated *V. latifii* is an extremely polymorphic taxon while the more widespread *albicornuta* is monomorphic, but in this case it is a unique pattern not found in *latifii*. As stated earlier, it is in many ways similar to the pattern type found in the *xanthina* stem (including the Iranian *wagneri*), and thus a symplesiomorphic character state, uniting the *raddei* and *xanthina* species-groups. However, it may also be a case of convergence, even though this is less probable as traces of the same kind of pattern can be seen in most taxa in the *raddei* species-group (see above).

A vicariance hypothesis based on sympatric herpetofauna, for the present pattern of the two subspecies of *raddei* and of *V. albicornuta* and *V. latifii*, is at present more difficult to analyse, with only the fragmented knowledge of the local herpetofaunas. Some patterns of sympatry can be obtained from the literature, which support vicariance rather than dispersal explanations. Although occurring in different habitats, the east Azarbaijan form of *Elaphe longissima* ssp. (Nilson & Andr n 1984a) seems to have the same distribution as *V. raddei kurdistanica*, while the north Iranian *Elaphe persica* (*E. longissima persica*) has a sympatric distribution with both *latifii* and *albicornuta*. Even more striking is the sympatric occurrence in this region of the three subgroups of *Vipera ursinii eriwanensis* (*V. u. ebneri*) (Saint Girons 1980; Joger 1984), which seems to be sympatric with both of the two subspecies of *raddei* as well as with *V. latifii*. Several other species are divided in two-area patterns, with perhaps *Lacerta raddei* — which occurs sympatric in the same habitat as *V. latifii* (with subspecies *L. r. defilippi*) and *Vipera r. raddei* (together with subspecies *Lacerta r. nairensis*) — as most characteristic, indicating relative recency of common ancestral biotas.

FUTURE DISPERSALS

Vipera xanthina has rather recently (Pleistocene) expanded into western Turkey, but has been stopped at the Pleistocene shores of the Aegean Sea. The only area where it has gone further west and into Europe is in Turkish Thrace and adjacent Macedonia (Greece), where in the latter area it has been discovered in two different places recently. *V. xanthina* seems to have the broadest ecological adaptability among all the vipers concerned, and the presumption by Sochurek (1984) that it will be found in southeast Bulgaria is perhaps plausible.

Vipera bornmuelleri has a rather fragmented occurrence in the mountain chains of Lebanon and Syria/Israel, restricted to a narrow zonation, and probably cannot disperse further due to ecological and biogeographical reasons. On the contrary, the situation seems to be rather serious for *bornmuelleri* due to habitat loss (overgrazing and clearance of cedar forests) and to warfare (Groombridge 1986).

Vipera wagneri and *V. bulgardaghica* probably have only fragmentary distributions and may even be extinct. No living specimens of these taxa have been found during this century. The Bulgar Dag (Bolkar Dag) mountains, the habitat for *bulgardaghica* consist of Paleozoic and old Mesozoic crystalline limestone and marble, which are weathered heavily (Güldali 1979), leaving only remnants of hard rocks. The habitat for this species seems to be disappearing for geological reasons.

Vipera raddei seems to have rather dense populations within its range, and is probably successful in the rather rocky habitat that characterizes this species (although much reduced in recent times due to overcollecting). The narrow habitat choice may, however, prevent it from further expansion of its range, as most of the areas surrounding the present habitat are sandy hills or dry plains (Darevsky 1966; Flärdh 1983; Groombridge 1986; own observations). The southern subspecies *kurdistanica* may, however, occur further west into Turkey, or may disperse in that direction in the future as suitable habitats can be found there (own observations).

Not much can be said at present about the situation for *V. albicornuta*, while *V. latifii* seems to be rather restricted to the central Alburz range and will probably not extend its range. In fact, it is seriously threatened for various reasons and may even disappear totally from its range in the future. First, it is probably submitted to serious competition with *Agkistrodon intermedius caucasicus*, which occupies the same niche in the same microhabitat, and which seems to be more successful as it also occupies all the different surrounding habitats (Andrén & Nilson 1979). Second, a large part of the known range, the Lar valley, is now changed into a huge water reservoir and, in the remaining unsubmerged parts of the valley, the microclimate is likely to have been altered. Up to now, however, these species seem to have been rather abundant. The number of specimens collected for venom extraction has been large. Between 1969 and 1973 about 7,900 specimens of *V. latifii* and about 1,680 specimens of *V. albicornuta* had been collected for the Razi serum institute in Iran (Latifi & Farzanpay 1973). Up to 1978 around 9,400 specimens of *V. latifii* and 4,400 specimens of *V. albicornuta* had been collected for this purpose (Latifi 1978).

OCCURRENCE OF SYMPATRIC VIPERS

Vipera ammodytes has, by several authors (e.g. Tristram 1888; Boulenger 1896, 1913; Schwarz 1936; Bodenheimer 1944; Mertens & Wermuth 1960; Klemmer 1963; Eiselt & Baran 1970; Baran 1976; Basoglu & Baran 1980; Saint Girons 1978, 1980), been considered to occur sympatrically with the *xanthina* species-group in southern Turkey, Syria, and Lebanon. It is, however, doubtful if this species really occurs in the whole of this region. There are few indications of this, and the only recent record is an exuvia of this species from Kusadasi in western Anatolia (Eiselt & Baran 1980), which is at present the only published evidence of true sympatry of *xanthina* and *ammodytes* in Anatolia. All other records are of old age and not always reliable.

Boettger (1880) claimed that *V. ammodytes* was common in the Lebanon mountains, but according to Werner (1939) there is no doubt that this species in Lebanon is identical with *V. xanthina* (= *bornmuelleri*). Boulenger (1913) described two specimens of *Vipera ammodytes meridionalis* from Syria and one from Lebanon. The "Lebanon" specimen was originally labelled Syra (Haas 1951) and then changed into Lebanon, probably in misreading Syra for Syria. Syra is a Greek island in the Aegean Sea and a part of the range for *V. ammodytes meridionalis* (Beutler & Frör 1980). The pholidosis of the three specimens from "Syria" (Boulenger 1913) agrees well with data given by Wettstein (1953) for specimens of *V. ammodytes meridionalis* from the Aegean Sea.

Schwarz (1936) mentioned an observation of *V. ammodytes*, southeast of Konya in southern Anatolia. Currently there are published observations of vipers which have shown to be misidentifications of other species of vipers or even confusions with colubrids such as *Coluber nummifer* (e.g. Wettstein 1967). *Vipera ammodytes* can also superficially be very similar to *V. xanthina*. However, recent information from a professional Turkish snake catcher verifies the occurrence of *V. ammodytes* in Konya (Flärdh, pers. comm.).

There remains a specimen in the Natural History Museum in Wien (NMW 13200) which was bought from H. Rolle, and which has "Cilicien" as sole locality (Eiselt & Baran 1970). This specimen agrees also with *V. ammodytes meridionalis* from Greece in morphology and, even though the record cannot be eliminated at present, the possibility of an originally wrong locality or exchange of labels cannot be excluded. In spite of much searching in the Taurus range (south of Konya, Cilicia) (e.g. Venzmer 1917, 1923; Bird 1936; Bodenheimer 1944; Eiselt 1965, 1967; Clark & Clark 1973; Baran 1976, 1982; and by us, during 1982, 1983, and 1984), no further specimens of *V. ammodytes* have been obtained. These two last records of *V. ammodytes* from Konya and the Taurus range are from regions east of the known range for *V. xanthina* s. str. but west of the locality of *V. bulgardaghica*, i. e. from a region where no other vipers have been reported. Thus, a picture emerges where the related *V. xanthina* and *V. bulgardaghica* are geographically separated by a region which may be inhabited, although sparsely, by *V. ammodytes*.

Occasionally, however, *Vipera ammodytes* may be sympatric with *V. xanthina*. The two species have on a few occasions been reported from the Istanbul area and just south of the Marmara Sea (e.g. Baran 1976) and from the northeastern Greek mainland where they should be sympatric. However, too few records of either species have been made to allow any conclusion of niche overlap or potential competition. The differences in main distribution of *Vipera ammodytes* and *V. xanthina* in Turkey indicate the occurrence of diffuse competition. Both species are of similar size, feed on small rodents and inhabit mostly rocky or stony habitats with a varying vegetation cover.

Two other species of the *xanthina* group (*bulgardaghica* and *bornmuelleri*) have sympatric distributions with the large *V. lebetina obtusa* and *V. palaestinae*, but the former two are montane and inhabit much higher altitudes. In the Cilician Taurus, *V. bulgardaghica* occurs in areas around 2,500 m altitude, while *V. lebetina obtusa* has

so far only been found in the Adana lowland plains south of the mountains. (We have found the latter at 1,300 m altitude at Gaziantep.) *V. lebetina obtusa* also occurs in northern and central Lebanon but only at lower altitudes (Zinner 1967; BM specimens). *V. palaestinae* is also found at lower altitudes such as the coastal plains (Zinner 1967), while *bornmuelleri* occurs at higher altitudes. On Mt. Hermon, *V. bornmuelleri* is restricted to an elevation of between 1,800 and 2,800 m while *V. palaestinae* occurs below 1,600 m altitude (Werner & Avital 1980).

Another viper within the range of *V. xanthina* is *V. ursinii anatolica* from Ciglikara, Elmali, SW Turkey, where it is sympatric with *V. xanthina*. These two species have, however, completely separate niches.

As the exact distribution of *V. wagneri* is unknown, nothing can be said about sympatry with other vipers. But *V. ursinii* and *V. raddei* occur in the regions of northwestern Iran and may be sympatric. This may also be true for *Vipera lebetina*.

In Turkey and the USSR, *V. raddei* is sympatric with *V. lebetina obtusa* and with *V. ursinii eriwanensis*, but there seems to be an altitudinal separation with *raddei* ranging in intermediate zonations. *Vipera ammodytes transcaucasiana* has recently been found in the Kars territory of Turkey (Billing, pers. comm.), which also is part of the range of *V. raddei*.

Pseudocerastes persicus may intervene with the distribution of *V. raddei kurdistanica*, but the former inhabits a drier and less rocky habitat, and the actual distribution and occurrence of *Pseudocerastes* in this region of Iran are far from clear.

Vipera latifii is sympatric in the same microhabitat with *Agkistrodon intermedius caucasicus* in the Lar valley in north Iran. We have seen the two species basking at the same spot, and a pronounced competition must occur between these species. Also *V. ursinii eriwanensis* can be found in the Lar valley, but in a different habitat than *V. latifii*. *Vipera lebetina obtusa* can be found at lower altitudes in the Alburz mountains, while *Pseudocerastes persicus* and *Echis carinatus sochureki* are found just south of the mountains (Nilson & Andrén 1981).

Vipera albicornuta may intervene with *V. lebetina obtusa* and *Pseudocerastes persicus* (Latifi 1984), but is probably found in different habitats.

LITERATURE CITED

- Andrén, C., & G. Nilson (1976): Observations on the herpetofauna of Turkey in 1968—1973. — Brit. J. Herpetol. 5: 575—584.
- & — (1979): *Vipera latifii* (Reptilia, Serpentes, Viperidae) an endangered viper from Lar Valley, Iran, and remarks on the sympatric herpetofauna. — J. Herpetol. 13: 335—341.
- Arnold, E. N. (1973): Relationships of the palaearctic lizards assigned to the genera *Lacerta*, *Podarcis*, *Algyroides* and *Psammodromus* (Reptilia, Lacertidae). — Bull. Brit. Mus. Nat. Hist. (Zool.) 25: 289—366.
- Bannikov, A. G., I. S. Darevsky, W. G. Iszczenko, A. K. Rustamov & N. N. Shcherbak (1977): *Opredelitelj zemnovodnyh i presmykajuscichsja fauny SSSR*. Moskow, 414 pp.
- Baran, I. (1976): Türkiye yılanlarının taksonomik revizyonu ve coğrafi dağılımları. — TBTA Yayınları No 309, T.B.A.G. seri No 9, Ankara, 177 pp.
- (1982): Zur Taxonomie der Schlangen in Südost- und Ost-Anatolien. — Spixiana 5: 51—59.
- Basoglu, M., & I. Baran (1977): Türkiye Sürüngenleri. I. Kaplumbaga ve kertenkeleler. — Ege Üniv. Fen. Fak. Kitapl. Ser., Bornova 76: 1—255.
- & — (1980): Türkiye Sürüngenleri. II. Yılanlar. — Ege Üniv. Fen. Fak. Kitapl. Ser., Bornova 81: 1—218.
- Beutler, A., & E. Frör (1980): Die Amphibien und Reptilien der Nordkykladen (Griechenland). — Mitt. Zool. Ges. Braunau 3: 255—290.
- Bird, C. G. (1936): The distribution of reptiles and amphibians in Asiatic Turkey, with notes on a collection from the Vilayets of Adana, Gaziantep and Malatya. — Ann. Mag. Nat. Hist. London. 18: 257—281.
- Bodenheimer, F. S. (1944): Introduction into the knowledge of the Amphibia and Reptilia of Turkey. — Rev. Fac. Sci. Univ. Istanbul, Sér. B 9: 1—78.
- Boettger, O. (1880): Die Reptilien und Amphibien von Syrien, Palästina und Cypern. — Ber. Senck. naturf. Ges. Frankfurt 1880: 132—219.
- (1890): Eine neue Viper aus Armenien. — Zool. Anz. 13: 62—64.
- Bolkay, S. J. (1913): Additions to the fossil herpetology of Hungary from the Pannonian and Praeglacial Period. — Mitt. Jahrb. kgl. ungar. Geol. Reichsanst. 21: 217—230.
- (1920): O razvojnomo redu *Vipera Gedulyi* By.-*Vipera ammodytes* L.-*Vipera meridionalis* Blgr. — Glasnik Zemaljsk. Mus. Bosni Herceg. 32: 1—12.
- Boulenger, G. A. (1896): Catalogue of the snakes in the British Museum, Vol. III. — Trustees of the British Museum London, 575 pp.
- (1913): The Snakes of Europe. London, 269 pp.
- Braattstrom, B. H. (1964): Evolution of the pit vipers. — Trans. San Diego Soc. Nat. Hist. 13: 185—268.
- Butzer, K. W. (1958): The Near East during the last glaciation. A palaeogeographical sketch. — Geogr. J. 124: 367—369.
- Clark, R. J. (1969): A collection of snakes from Greece. — Brit. J. Herpetol. 4: 45—48.
- (1972): New locality records for Greece reptiles. — Brit. J. Herpetol. 8: 311—312.
- Clark, R. J., & E. D. Clark (1973): Report on a collection of amphibians and reptiles from Turkey. — Occ. Pap. Calif. Akad. Sci. 104: 1—62.
- Corkill, N. L. (1932): The snakes of Iraq. — J. Bombay Nat. Hist. Soc. 35: 552—572.
- Darevsky, I. S. (1966): Ecology of the Rock-viper (*Vipera xanthina raddei* Boettger) in the natural surroundings of Armenia. — Mem. Inst. Butantan Simp. Internac. 33: 81—83.
- Dowling, H. G. (1951): A proposed standard of counting ventrals in snakes. — Brit. J. Herpetol. 1: 97—99.
- Eiselt, J. (1965): Bericht über eine zoologische Sammelreise nach Südwest-Anatolien im April/Mai 1964. — Ann. Naturhist. Mus. Wien 68: 401—406.
- (1967): Bericht über eine dritte zoologische Sammelreise in der Türkei, April bis Juni 1966. — Ann. Naturhist. Mus. Wien 70: 293—300.

- Eiselt, J., & I. Baran (1970): Ergebnisse zoologischer Sammelreisen in der Türkei: Viperidae. — Ann. Naturhist. Mus. Wien 74: 357—369.
- Erol, O. (1976): Quaternary shoreline changes on the Anatolian coasts of the Aegean Sea and related problems. — Bull. Soc. géol. France. 18: 459—468.
- Esterbauer, H. (1985): Zur Herpetofauna Südwestsiriens — Herpetofauna 7: 23—34.
- Flärdh, B. (1983): Herpetofaunan på Mount Ararat. — Snoken 13: 31—38.
- Gärdenfors, U. (1980): Ein Nachweis von *Vipera xanthina* in Griechenland (Reptilia: Serpentes: Viperidae). — Salamandra 16: 270.
- Gray, J. E. (1849): Catalogue of the specimens of snakes in the collection of the British Museum. London, 125 pp.
- Greuter, W. (1970): Zur Paläogeographie und Florengeschichte der südlichen Ägäis. — Feddes Repertorium 81: 233—242.
- Grillitsch, B., & F. Tiedemann (in press): Zur Verbreitung von *Vipera xanthina* in Griechenland. — Salamandra.
- Groombridge, B. C. (1980): A phyletic analysis of Viperine snakes. Unpublished Ph. D. Thesis, City of London Polytechnic/British Museum (Nat. Hist).
- Groombridge, B. C. (1986): The IUCN Amphibia-Reptilia Red Data Book. Part 2 (in press).
- Güldali, N. (1979): Geomorphologie der Türkei. — Beihefte zum Tübinger Atlas des Vorderen Orients. Reihe A, No. 4, 265 pp.
- Haas, G. (1951): On the present state of our knowledge of the herpetofauna of Palestine. — Bull. Res. Council. Isr. 1: 67—95.
- (1952): Remarks on the origin of the herpetofauna of Palestine. — Rev. Fac. Sci. Univ. Istanbul, Ser. B, 17: 95—105.
- Hammond, A. L. (1976): Paleoclimate: Ice age earth was cool and dry. — Science 191: 455.
- Hennig, W. (1966): Phylogenetic systematics. — University of Illinois Press, Urbana, 363 pp.
- Hoofien, J. H. (1968): Contributions to the herpetofauna of Mount Hermon. No. II. — Isr. J. Zool. 17: 199—204.
- (1973): Contributions to the herpetofauna of Mount Hermon. No. IV. — Isr. J. Zool. 22: 67—73.
- Hraqui Bloquet, S. (1981): Les reptiles du Liban. 1. Nomenclature et note écologique. — Ecologia Mediterranea 7: 93—101.
- Hurvitz, E. (1980): Checklist of vertebrates on Mt. Hermon. In: A. Shmida and M. Livne (eds.): Mt. Hermon Nature and Landscape. — HaQibbuz HaMeuhad: 230—239 (in Hebrew).
- Joger, U. (1984): The venomous snakes of the Near and Middle East. — Beihefte zum Tübinger Atlas des Vorderen Orients. Reihe A, Nr. 12, 115 pp.
- Kevoork, O. K. (1972): *Rana camerani* Boulenger from Iraq. — Bull. Iraq nat. Hist. Mus. 5: 9—15.
- Klemmer, K. (1963): Liste der rezenten Giftschlangen. — Behringwerk-Mitteilungen, Sonderband „Die Giftschlangen der Erde“: 255—464.
- Latifi, M. (1978): Commercial production of anti-snakebite serum (Antivenin). In: Biology of the Reptilia (eds. Gans, D., & K. A. Gans) 8: 561—588.
- (1984): Variation in yield and lethality of venoms from Iranian snakes. — Toxicon 22: 373—380.
- Latifi, M., & R. Farzany (1973): Yield of venom and distribution of Iranian venomous snakes. — Pahlavi med. J. 4: 556—564.
- Latifi, M., A. R. Hoge & M. Eliazan (1966): The poisonous snakes of Iran. — Mem. Inst. Butantan Simp. Internac. 33: 735—744.
- Lorch, J. (1959): A preliminary report on the pollen flora of Lake Hula. — Bull. Res. Council. Israel, 7 D: 87—89.
- Louis, H. (1944): Die Spuren eiszeitlicher Vergletscherung in Anatolien. — Geol. Rundsch. 442—481.
- Marx, H., & G. B. Rabb (1970): Character analysis: an empirical approach applied to advanced snakes. — J. Zool. London 161: 525—548.

- & — (1972): Phyletic analysis of fifty characters of advanced snakes. — *Fieldiana Zool.* 63: 1—321.
- M a y r , E. (1969): *Principles of Systematic Zoology*. — McGraw-Hill, New York, 428 pp.
- M e l c h i o r , H. (1937): Zur Pflanzengeographie des Elburs-Gebirges in Nord-Iran. — *Sitz. Ges. naturf. Freunde Berlin* 113: 55—73.
- M e r t e n s , R. (1951): Die Levante-Otter der Cycladen. — *Senckenbergiana* 32: 207—209.
- (1952): Amphibien und Reptilien aus der Türkei. — *Rev. Fac. Sci. Univ. Istanbul (Ser. B)* 17: 41—75.
- (1967): Über *Lachesis libanotica* und den Status von *Vipera bornmuelleri*. — *Senck. biol.* 48: 153—159.
- M e r t e n s , R., & H. W e r m u t h (1960): Die Amphibien und Reptilien Europas; dritte Liste, nach dem Stand vom 1. Januar 1960. Frankfurt/M., 264 pp.
- M e r t e n s , R., I. S. D a r e v s k y & K. K l e m m e r (1967): *Vipera latifii*, eine neue Giftschlange aus dem Iran. — *Senck. biol.* 48: 161—168.
- M ü l l e r , L., & O. W e i t t s t e i n (1933): Amphibien und Reptilien vom Libanon. — *Sb. österr. Akad. Wiss. Wien, math.-nat. Kl.* 142: 133—144.
- N i l s o n , G., C. A n d r é n (1981): Die Herpetofauna des Kavir-Schutzgebietes, Kavir-Wüste, Iran. — *Salamandra* 17: 130—146.
- & — (1984 a): A taxonomic account of the Iranian ratsnakes of the *Elaphe longissima* species-group. — *Amphibia-Reptilia*, 5: 157—171.
- & — (1984 b): Systematics of the *Vipera xanthina* complex (Reptilia: Viperidae). II. An overlooked viper within the *xanthina* species-group in Iran. — *Bonn. zool. Beitr.* 35: 175—184.
- & — (1985 a): Systematics of the *Vipera xanthina* complex (Reptilia: Viperidae). I. A new Iranian viper in the *raddei* species-group. — *Amphibia-Reptilia*, 6: 206—214.
- & — (1985 b): Systematics of the *Vipera xanthina* complex (Reptilia: Viperidae). III. Taxonomic status of the Bulgar Dag viper in south Turkey. — *J. Herpetol.* 19: 276—283.
- N i l s o n , G., & P. S u n d b e r g (1981): The taxonomic status of the *Vipera xanthina* complex. — *J. Herpetol.* 15: 379—381.
- O b s t , F. J. (1983): Zur Kenntnis der Schlangengattung *Vipera* (Reptilia, Serpentes, Viperidae). — *Zool. Abh. staatl. Mus. Tierkde. Dresden* 38: 229—235.
- O n d r i a s , J. C. (1969): The occurrence of *Vipera xanthina* in the island of Chios, Greece. — *Biol. Gallo-Hellen. Athen* 2: 185—187.
- P e t e r s , G. (1962): Die Zwergeidechse (*Lacerta parva* Boulenger) und ihre Verwandtschaftsbeziehungen zu anderen Lacertiden, insbesondere zur Libanon-Eidechse (*L. fraasii* Lehrs). — *Zool. Jahrb. Syst., Jena*, 89: 407—478.
- P f a n n e n s t i e l , M. (1954): Die Schwankungen des Mittelmeerspiegels als Folge der Eiszeiten. Freiburg im Breisgau, 19 pp.
- P i c a r d , L. (1937): Inferences on the problem of the Pleistocene climate of Palestine and Syria drawn from flora, fauna and stratigraphy. — *Proc. prehist. Soc.* 5: 58—70.
- (1943): Structure and evolution of Palestine. — *Bull. geol. Dept. Hebr. Univ., Jerusalem IV*, Nos. 2—4.
- P i e p e r , H. (1970): Neue Beiträge zur Kenntnis der Herpetofauna der südägäischen Inseln. — *Senck. biol.* 51: 55—65.
- P l a t n i c k , N. I., & G. Nelson (1978): A method of analysis for historical biogeography. — *Syst. Zool.* 27: 1—16.
- R a g e , J. (1976): Les squamates du Miocène du Béni Mellal, Maroc. — *Geol. méditerranéenne* 3: 57—69.
- R e e d , C. A., & H. M a r x (1959): A herpetological collection from northeastern Iraq. — *Trans. Kansas Acad. Sci.* 62: 91—122.
- S a i n t G i r o n s , H. (1978): Morphologie externe comparée et systématique des vipères d'Europe (Reptilia, Viperidae). — *Rev. Suisse Zool.* 85: 565—595.

- (1980): Biogéographie et évolution des vipères européennes. — C. R. Soc. Biogéogr. 496: 146—172.
- Schätti, B., & A. Agasian (1985): Ein neues Konzept für den *Coluber ravergeri*-*C. nummifer*-Komplex (Reptilia, Serpentes, Colubridae). — Zool. Abh. 40: 109—123.
- Schneider, B. (1975): Eine mittelpleistozäne Herpetofauna von der Insel Chios, Ägäis. — Senck. biol. 56: 191—198.
- (1983): Zur Herpetofauna der Insel Kalymnos und Telentos (Dodekanes, Ägäis). — Salamandra 19: 61—70.
- Schwarz, E. (1936): Untersuchungen über Systematik und Verbreitung der europäischen und mediterranen Ottern. — Behringwerk-Mitt. 7: Die europäischen und mediterranen Ottern und ihre Gifte: 159—362.
- Sitar, V. (1964): Report on the phytopalaeontological investigations of the Tertiary deposits in the vicinity of Orivnica (Southern Slovakia). — Geol. Sborn. Bratislava 15: 75—78.
- Sneath, P.H.A., & R.R. Sokal (1973): Numerical taxonomy. San Francisco, 573 pp.
- Sochurek, E. (1984): Die Giftschlangen der Türkei — eine Übersicht. — Elaphe, Aquar. Terr. Beiträge, 1/84: 1.
- Strauch, A. (1869): Synopsis der Viperiden, nebst Bemerkungen über die geographische Verbreitung dieser Giftschlangen-Familie. — Mém. Acad. imp. Sci. St.-Petersbourg (7) 14: 1—144.
- (1873): Die Schlangen des Russischen Reiches, in systematischer und zoogeographischer Beziehung. — Mém. Acad. imp. Sci. St.-Petersbourg (7) 21: 1—188.
- Szyndlar, S. (1984): Fossil snakes from Poland. — Acta zool. Cracov. 28: 1—156.
- Tristram, H. B. (1888): The Survey of Western Palestine: The Fauna and Flora of Palestine. The Committee of the Palestine Exploration Fund, London, XXII + 455 pp.
- Trutnau, L. (1975): Europäische Amphibien und Reptilien. — Stuttgart, 212 pp.
- (1981): Schlangen im Terrarium. Band 2. Giftschlangen. Stuttgart, 200 pp.
- Venzmer, G. (1917): Zur Schlangenfauna Süd-Kleinasiens, speziell des cilicischen Taurus. — Arch. Nat. gesch. Berlin, A(11) 83: 95—122.
- (1922): Neues Verzeichnis der Amphibien und Reptilien von Kleinasien. — Zool. Jb. Syst. 46: 43—60.
- Wagner, M. (1868): Die Darwin'sche Theorie und das Migrationsgesetz der Organismen. Leipzig, 62 pp.
- (1889): Die Entstehung der Arten durch räumliche Sonderung. Basel, 667 pp.
- Weinstein, S. A., & S. A. Minton (1984): Lethal potencies and immunoelectrophoretic profiles of venoms of *Vipera bornmulleri* and *Vipera latifii*. — Toxicon 22: 625—629.
- Werner, F. (1898): Über einige neue Reptilien und einen neuen Frosch aus dem cilicischen Taurus. — Zool. Anz. 21: 217—223.
- (1914): Zur Herpetologie der Türkei. — Zool. Anz. 43: 497—499.
- (1922): Synopsis der Schlangenfamilien der Amblycephalidae und Viperidae. — Arch. Nat. gesch. 88 A: 185—244.
- (1938): Eine verkannte Viper (*Vipera palaestinae* n. sp.). — Zool. Anz. 122: 313—318.
- (1939): Die Amphibien und Reptilien von Syrien. — Abh. Ber. Mus. Naturkd. Vorgesch. Magdeburg 7: 211—223.
- Werner, Y. L., & E. A vital (1980): The herpetofauna of Mt. Hermon and its altitudinal distribution. — Isr. J. Zool. 29: 192—193.
- Wettstein, O. (1953): Herpetologia aegae. — Sp. Akad. Wiss. Wien (Math. -naturw. Kl., Abt. 1) 162: 651—833.
- (1967): Rectifications to: J.F.D. Frazer, "Herpetological notes on Rhodes". — Brit. J. Herpetol. 3: 313—314.
- Yablokov, A.V., A.S. Baranov & A.S. Rozanov (1980): Population structure, geographic variation, and microphylogenesis of the sand lizard (*Lacerta agilis*). — Evolutionary Biology (eds. Hecht, M. K., W. C. Steere & B. Wallace) 12: 91—127.

- Z i n n e r , H. (1967): Herpetological collection trips to the Lebanon 1965 and 1966. — Isr. J. Zool. 16: 49—58.
- (1972): Contribution to the Herpetofauna of Mount Hermon. No. III. — Isr. J. Zool. 21: 123—127.
- Z o h a r y , M. (1973): Geobotanical Foundations of the Middle East. Vol. 1 and 2. Stuttgart, 739 pp.

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